Food Preferences of the European Hare (*Lepus europaeus* Pallas) on a fescue grassland.

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ABSTRACT

Diet of the European hare (*Lepus europaeus* Pallas) living on a fescue (*Festuca novae-zelandiae*) grassland in central high country Canterbury was examined using microscopical gut sample analysis. Availability of food plants was estimated by a monthly vegetation survey. Major dietary items were analysed for calorific value, neutral detergent fibre content (digestibility) and secondary metabolites (phenols, condensed tannins and monomeric tannins).

Hares in this area relied heavily on *Hieracium pilosella* as the major constituent of their diet. Grasses and tussocks made up the majority of the remaining food. The diet of females, males, juveniles and adults were all significantly different. Diet also varied throughout the year, although it largely reflected the availability of the various food items, except *Rhacomitrium lanuginosum* which was avoided. Food plant selection did not correlate with calorific value or secondary metabolite content. However, there was some correlation between the neutral detergent fibre content or digestibility of the plants measured and their level of consumption by the hares. It appears from the results of this study that the diet of hares in the study area is influenced predominantly by the availability of the various potential food plants but is also influenced by the digestibility of those plants available.

Chapter 1 : INTRODUCTION

1.1 Taxonomy

The order Lagomorpha contains rabbits, hares and pikas and was for a long time combined with the rodents, the group being dist inguished as the sub-order Duplicidentata, characterised by having a small second upper incisor (Southern 1964). Barrett-Hamilton (1912) placed hares and rabbits with the rodents but acknowledged that further subdivision was inevitable. The whole group was later revised and a new order was created after fossil evidence showed that the two divisions (rodents and the hares and rabbits) were distinct by the Eocene (about 60 million ybp) (Matthews 1952; Southern 1964). The current situation is Order: Lagomorpha, Family; Leporidae, and Genus; Lepus.

The lagomorphs are small to medium sized quadrapedal mammals clothed in soft fur. Many have a short tail but some are tail-less. They are digitigrade or digitigrade on the fore feet and plantigrade on the hind feet. The soles of all feet are fur covered and the toes each have a claw. A wide diastema is created due to the lack of canine teeth and the incisors are chisel shaped, open rooted and grow continuously. The dental feature distinguishing lagomorphs from rodents is the presence of an extra pair of incisors set behind the upper incisors in the lagomorphs, whereas rodents have only one pair of incisors in each jaw (Horne 1978). Other less marked skull features further distinguish the lagomorphs from rodents.

In lagomorphs most food passes through the digestive system twice. Refection occurs during the day (Watson and Taylor 1955), fecal material being reingested directly from the anus. It is thought that refection provides the animal with vitamin B produced by bacterial action in the caecum but not absorbed there (Matthews 1971).

The Order Lagomorpha contains two distinct families;

1. Ochotonidae

These are the pikas or mouse hares found in Eastern Europe, Asia and mountains of western North America. They have considerable skull differences from hares and rabbits (Southern 1964).

2. Leporidae

The family Leporidae contains nine genera and 52 species of rabbits and hares which have spread throughout the world, except Australia and New Zealand (where they have been introduced) (Southern 1964). They are specialised vegetarian animals some species of which tend to undergo marked fluctuations in numbers, often in regular cycles of about ten years (Southern 1964; Walker 1964). Hares belong to the largest genus, *Lepus*, with 26 species which inhabit most of Eurasia as far as Sumatra, Java, Formosa and Japan; most of Africa except the rain forest of the Congo and the region along the Gulf of Guinea to the Atlantic coast; and most of North America, south to the Mexican Plateau, although their distribution is limited in the eastern half of the United States. After introduction by man they have further expanded their range and become common in areas of South America, New Zealand, islands off the coast of

Africa and some parts of the eastern United States (Walker 1964).

There is some confusion as to the exact nomenclature of the common brown hare, Lepus europaeus Pallas. Angermann (1983) and Flux (1983) both consider L. europaeus and L. capensis to be insufficiently morphologically different to be positively separated. However, there remains confusion as to the correct nomenclature (Flux 1983) so I have continued to use L. europaeus in this study. The species ranges throughout Europe, Western Asia, Asia Minor and Iran. It has been introduced to Scandanavia, Finland, Australia, New Zealand, Chile and the Great Lakes area of North America (Southern 1964).

Hares are solitary animals which do not dig burrows for either shelter or to house their young. They spend the daylight hours resting in forms (slight depressions) amo ng vegetation. Leverets are born fully furred, with eyes open and can move about soon after birth. Each leveret then disperses and finds its own form but continues to be fed by the doe for some time afterwards. The period of feeding by the doe varies but peak milk production in captive hares has been found to reach a maximum after about 20 days and then decrease until the leverets are weaned. Leverets may begin to eat solid food as early as seven days after birth (Martinet and Demarne 1984).

1.2 Introduction and Distribution of hares in New Zealand

A subspecies of hare, *Lepus europaeus occidentalis* de Winton, or the common brown hare, was introduced into New Zealand in 1851 at Lyttleton (Donne 1924). Shortly afterwards a population was established on Banks Peninsula. During the following 20 years several importations were made from both Britain and Australia (Thompson 1922) to provide sport and also to improve the food supply of the early settlers. Many liberations were also made by private individuals (Wodzicki 1950).

The distribution of hares has not changed to any significant degree (except in South Westland (J. Parkes pers comm.)) since the initial rapid increase in numbers and spread. The eastern areas of both islands typically support far greater numbers of hares than do the western regions due to the more favourable climate in the drier eastern areas. Hares have not been introduced to any of the offshore islands, including Chatham Island and Stewart Island (Flux 1970). According to Wodzicki (1950) cover, together with altitude, climate, probably soil drainage and perhaps certain farming practices are the main factors determining the distribution of hares. The favoured habitat is thought to be scrub and native grasslands both below and above the timberline with agricultural land a secondary habitat only (Gibb and Flux 1973).

In favourable tussock country hares reach much higher altitudes than rabbits. In Central Otago they are reported up to 7000 feet (2100m), with quite a number above snowline (Wodzicki 1950). Habitation of these high altitude areas by *L. europaeus* appears to be restricted to New Zealand. In Europe L. timidus replaces L. europaeus at altitudes greater than 600m (Southern 1964).

In summary, hares after their initial increase in numbers have now reached a more or less stable position. The population has filled the suitable areas and is now subject only to inherent fluctuations and to changes induced by control measures and other limiting factors such as weather and predators (Wodzicki 1950). Because hares live totally above ground the weather factor can have a major effect on the survival of any age class through the winter (Amaya et al 1979). However, Keith (1979) states that food and predators appear to exert the strongest impact on hare survival.

1.3 Previous research

The biology of the various species of Lepus has been extensively studied for many years, with research focusing primarily on Lepus timidus (the mountain hare) and L. californicus (the snowshoe hare). The diet of the various species of hares, particularly these two species, has been extensively studied in North America, Europe and Britain (Hewson 1962, 1976; Currie and Goodwin 1966; Myrcha 1968; Flinders and Hansen 1972; Flinders and Crawford 1977; Parker 1977; Bryant 1979; Pehrson 1979; Sinclair et al 1982; Homolka 1987).

While a significant amount of literature has appeared overseas, in New Zealand studies of L. europaeus (the brown hare) have been relatively restricted. Flux has described the timing of the breeding season (1965(a)), the incidence of ovarian tumors (1965(b)), the occurrence of a white wrist band (1966), reproduction and body weights (1967(a)) and numbers and diet in an alpine basin (1967(b)). Parkes has described home ranges (1984) and annual patterns in reproduction and condition (1989). Other authors include Douglas (1970) concerning the movement of hares in the high country and Horne (1978) concerning seasonal and altitudinal variations in diet and abundance.

The greater research effort put into lagomorph biology in other countries reflects their great value as game animals in these countries. The situation is reversed in New Zealand where they are regarded primarily as a pest, and research has consequently tended to concentrate on aspects concerned with control rather than general biology (eg. Parkes 1981).

Other aspects of hare ecology relating to feeding have been investigated, again mostly by overseas workers, including nutritional studies by Holter et al (1974) and Lindlof et al (1974), a preference study by Radwan and Campbell (1968) and the effects plant secondary compounds have on feeding preferences and levels (Bryant 1981; Sinclair and Smith 1984; Tahvanainen et al 1985; Sinclair et al 1988).

The two diet studies in New Zealand (Flux (1967(b)) and Horne (1978)) were made on animals living in higher altitude grasslands containing snow tussock (Chionochloa spp.) in contrast to the fescue grassland in this study.

The population of hares used in this study was in the same location as that investigated by Douglas (1970) and Parkes (1981, 1984, 1989) and the study adds to comprehensive information on this particular population inhabiting a modified grassland in central Canterbury.

1.4 Aims of this study

The study had four aims:

1. A diet study to determine what plants are eaten and in what quantities.

2. A survey of the grassland plants for frequency of occurrence and approximate ground cover. Combined with the diet study this would reveal any preferences the hares have for particular plant species.

3. Determination of the potential annual growth of the grassland. Comparison of the actual annual growth with this result would reveal the amount being removed, mainly by hares.

4. Investigation to determine if any preference for particular plant species is based on nutritional value, digestibility or the occurrence of secondary metabolites (principally phenols).

Chapter 2 : STUDY AREA

2.1 Introduction

The study site was chosen because of the extensive research already completed on the hare population present (eg. Douglas 1970, Parkes 1984, 1989), the relatively large numbers of hares present and the nature of the riverflat which was suitable for the placement of plots for experiments. Also the vegetation of the riverflat is typical of many sites in the high country of Canterbury where hares are present.

2.2 Locality

The study site was a 120 hectare riverflat ($43^{o}05'$E;$171^{o}26'$S) located in the lower reaches of the Avoca River at 700m asl. and about 1km upstream from its confluence with the Harper River (Fig 2.1).

The Avoca River (a 4th order catchment of the Rakaia River) is located in Central Canterbury, with its headwaters originating approximately 12km south-east of the main divide. The lower reaches of the Avoca River consist of a wide, braided shingle riverbed. The total length of the Avoca River from its source to its confluence with the Harper River is about 28km.

2.3 Physiography

Three mountain peaks in the river catchment are higher than 2200m with the main ridges 1800-2000m, while the lower reaches of the Avoca River are at 600-700m asl. Peaks immediately surrounding the study site range from 1300-2000m. Remnant glaciers and permanent snow are features of the higher peaks in the headwaters.

The basement rock in the area is strongly indurated greywacke underlying uncemented greywacke gravels, leading to general instability and locally severe erosion (Clarke 1986). Slopes in the area are generally steep and rugged with many rocky outcrops and small sharp gullies.

The valley floor of the Avoca River is bordered in its lower reaches by fairly extensive riverflats which generally extend from the base of a steep slope and are themselves reasonably flat.

Soils are strongly leached and skeletal and are mostly upland, alpine and podzolised yellow-brown earths (Gregg 1964; Warren 1967). The geology and sediment sources in the area have been described in detail by Mosely (1979) and Suggate and Wilson (1958).

2.4 Climate

The climate in the general study area is cool-temperate with harsh conditions in the upper sub-alpine and alpine

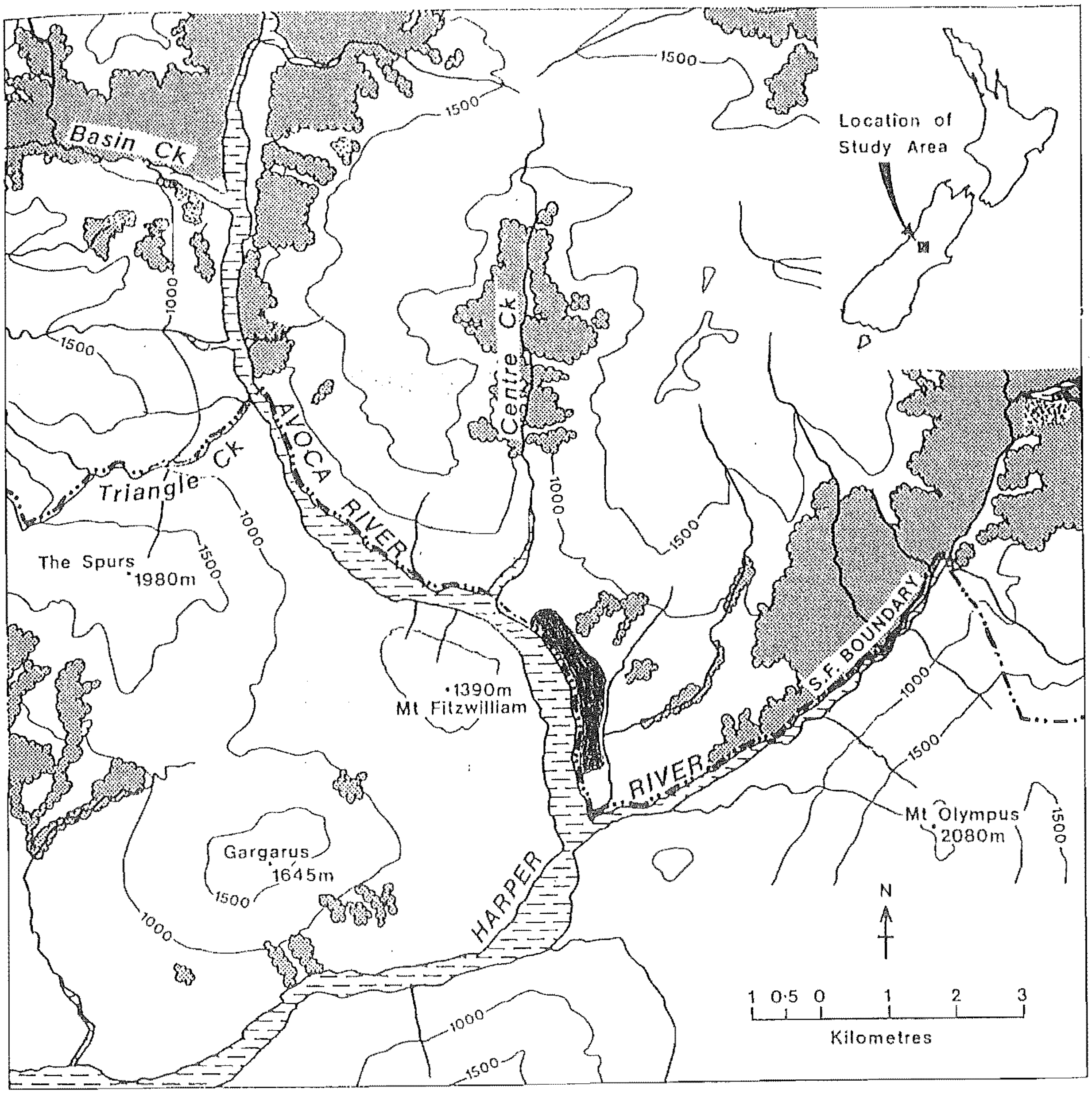


Figure 2.1: Location of the study site (heavily shaded area lower centre). Lighter shaded areas are remnant beech (*Nothofagus solandri* var *cliffortioides*) forest.

regions. As in the rest of New Zealand the dominant wind is from the westerly direction, with associated troughs which are frequent and persistent (up to 3 weeks), and are followed by fast moving, cold, south to south-west fronts, or by warmer anticyclones (DeLisle 1969; Clarke 1986). After the southerly front has passed there is often a period of showers (DeLisle 1969). North-west winds are also common in this area and are also often associated with rainfall.

Climate measurements are not available for the actual study site but recordings taken at 914m on the Craigieburn range (about 4km to the east) give an indication of the environmental conditions in the study area.

Rainfall increases with altitude and also towards the main divide. This gradient is pronounced with 8500mm annual precipitation falling near the main divide while the lower Avoca region (about 30-40km east of the main divide) receives 1000-1500mm. At Craigieburn rainfall averaged 1470mm per year, with an average of 129 days having greater than 1mm of rain. Rainfall has been estimated as 3700mm at timberline (1399m) a short distance upstream from the study site (Clarke 1986).

Air temperature varied considerably with the highest recorded value at Craigieburn being 32.9^{o}C and the lowest -9.6^{o}C. The average annual maximum was 29.2^{o}C. However the mean temperature of 8^{o}C is much lower than the maximum. Daily temperature variation is relatively great with an average of 10.7^{o}C. Ground temperature is relatively low with an average value of 0.3^{o}C but this is hardly surprising with 148.5 days of ground frost. Snow occurred at 914m on an average of 38.9 days but did not lie on the ground for extended periods. During the two year period of this study, snow remained on the study site for only five days during the winter of 1988. Gale force winds occurred on an average of 4.3 days and fog on 10.9 days at Craigieburn. Relative humidity was moderate at 76% (NZ met. service 1983).

2.5 Vegetation

The main factor influencing the general vegetation patterns in the Avoca River area is the strong west-east gradient of decreasing precipitation (Whitehouse et al 1983). The vegetation in the Avoca river area has been extensively modified in the past by humans and introduced grazing mammals. In the lower Avoca valley where the study site is located, the vegetation has been modified by Polynesian fires (Molloy et al 1963) and later by frequent fires to create sheep pasture (Packard 1947). These fires firstly removed the forest cover and, secondly, removed any subsequent regrowth. The result of these activities is that the lower valley is dominated by fescue grasslands. In the upper reaches of the valley, where the fires did not reach, extensive areas of mountain beech forest (*Nothofagus solandri* var *cliffortioides*) remain. Patches of beech forest remain in the lower valley but they are largely restricted to the mid to upper slopes. Areas above the bushline vary in plant composition, but three associations dominate. These are sub-alpine shrublands, snowgrass and herbfields, and scree areas.

In the riverflat study site fescue grasslands dominate with matagouri (*Discaria toumatou*) and sweet briar (*Rosa rubignosa*) locally extensive around the base of the hill. The induced fescue grassland has largely replaced the original beech forests and indigenous tall tussocks (*Chionochloa macra* and *C. pallens*) (Rose 1983). Dominant plants in this association are the tussock *Festuca novae-zelandiae* and the pasture grasses sweet vernal (*Anthoxanthum odoratum*), browntop (*Agrostis tenuis*) and yorkshire fog (*Holcus lanatus*). A vegetation gradient exists on the study flat with a moss (*Rhacomitrium lanuginosum*) dominated association occurring near the river on the more recently formed terraces. This grades to a fescue/browntop dominated association on the more fertile areas near the base of the hill. Between these two communities is a fescue/moss/*Hieracium* dominated association which makes up the major vegetation type in the area.

Hieracium spp. (*H. pilosella* and *H. lachenalii*) is a relative new comer to the grassland but is becoming more common as shown by Rose (1983). Over the last 20 years on the drier, lower valley sites the two *Hieracium* species together with *Anthoxanthum odoratum* have spread with a consequent reduction in native species and the amount of bare ground.

The only species of *Hieracium* present on the study site is *H. pilosella*. In lower valley sites such as the study site *H. lachenalii* tends to be restricted to the forest floor and damper areas (pers. obs.).

Chapter 3 : METHODS

3.1 INTRODUCTION

Many early diet studies of mammals were concerned only with qualitative aspects (eg. Cockayne 1919, Tribe 1950, Stoddart 1952, Hercus 1960), but more recently emphasis has been placed on quantitative assessment (eg. Stevens 1977, Nugent 1983, McLeod 1986) which has become possible due mainly to improved techniques. The diet of hares was determined by counting the number of cuticle fragments of each plant species remaining in the gut sample. This figure was then converted to a percentage of the total number of cuticle fragments identified and therefore of the total stomach contents.

The methods of diet analysis in mammals have been reviewed by Scotcher (1979) and Nugent (1983). Many forms of diet assessment have been tried in the past including direct observation, examination of material from fistulated animals, vegetation surveys before and after grazing and feeding on a free choice basis. However the most widely recognised method is that of microscopical analysis of faecal or stomach contents. Stomach content analysis is considered to be more accurate than faecal analysis as the ingested material has not been subjected to the full effects of the digestive system, which due to the digestive processes may remove a large proportion of the more fragile species.

Macroscopic identification of the plant species was not a possibility in this study as all particles had been well masticated and reduced to very small sizes. For this reason plant cuticles were identified under a microscope.

Hercus (1960) has summarised the advantages of identifying cuticles as the following:

1. The plant cuticle moulds itself to the contours of the underlying epidermal cells, allowing imprints to be left if it is removed.

2. The arrangement of the epidermal cells is characteristic of the plant family and often of the species.

3. The cuticle is impermeable to water and resistant to most chemicals and the action of microbial organisms. During digestion the cuticle is separated but remains unchanged, except for a reduction in overall size due to mechanical action.

Determination of diets to the species level by this method is time consuming however and the differential resistance of various cuticles can lead to biases. This technique is an established one (Harris and O'Connor 1980) recommended and used, for example, by the Tussock Grassland and Mountainlands Institute, Lincoln College. Combined with the great amount of time involved in undertaking a cuticle analysis study are the inherent pitfalls of the sampling method. Biases in the sampling method can begin with the collection of the gut samples. When samples are taken the stomach contents should be thoroughly mixed by massaging the stomach or alternatively several sub-samples should be taken from different areas of the gut (the method employed in this study). The sieving of samples has been shown to remove some plants or parts of plants (Rogerson et al 1976; Barker 1986(a)) so sieving should be kept to a minimum. During the analysis there are several factors to keep in mind to avoid over or under representation of the various plant species. Cuticle fragments covering more than half the field of view should be counted as two identifications and very small fragments should not be identified, due not only to the potential for overestimation of that species but also to the increased possibility of making an incorrect identification. Hansson (1970) has stated that even the most careful operator will inadvertantly overestimate the less common and underestimate the more common items. However, Westoby et al (1976) take the opposite view and conclude from their study that there was a tendency to underestimate or miss entirely taxa which were present in small amounts, and to overestimate those present in large amounts (due largely to the underestimation of the less common items). In an attempt to overcome this possible source of error Barker (1986(b)) has developed a technique in which the amount of a species is categorised as none, a little, some or a lot. Barker claims that this method is no less accurate than that of counting particles. However, it would appear that this method gives data more orientated to qualitative rather than quantitative analysis and therefore it was not employed in this study.

Although there appear to be many problems with the methods of cuticle analysis used in this study, it was considered that it would give the best results with regard to further analysis and comparisons between the various age and sex categories. Provided methods are kept constant any errors in the analysis should be kept to a minimum and the errors would be constant throughout the entire analysis.

A vegetation survey was undertaken to determine the availability of the various potential food plants. To try to answer the question of why particular plants were being eaten three seperate approaches were taken. The first was to determine the calorific value (or energy value) of the different plant species. The theory of optimal foraging states that an animal should choose to consume food items that return the maximum energy value while requiring expenditure of the minimal amount of energy (Pyke et al 1977). However, a plant may have a high calorific value but the nutrients may be largely locked up in unusually fibrous or indigestible substances. Therefore the second approach undertaken was to determine the digestibility of the various food items. As a plant may be high in calorific value and highly digestible but may have some substance such as a toxin to discourage herbivores, an analysis for secondary metabolites was also made.

3.2 DIET STUDY

3.2.1 Collection of gut samples

Seven hundred and thirty one hares were collected by J. Parkes of the Forest Research Institute from the river flat study site between 1976 and 1987, although some were taken from other similar flats further up the same river. Some samples (40 hares) were collected by me during 1987 to 1988. Most hares were shot during the evening and at night. A sample of mixed stomach contents of about 20mls was removed from each hare, preserved in 10% formalin and labeled according to sex, age (juvenile or adult), and date of collection.

Age determination was by extracting eye lenses which were then oven dried at 80^{o}C for four days (when they had ceased to lose weight), and weighed to the nearest milligram. Mean eye lense weight was then used to separate the animals into two age classes (Broekhuizen and Maaskamp 1979). Animals with eye lense weights less than 260mg in June and having been born during the current or previous breeding season before July 1 were classified as juveniles. Adults were all hares that had lived past 1 July. This date was chosen as all animals could be separated reliably into juvenile and adult classes by eye lense weights up to the end of June (Parkes 1989).

3.2.2 Preparation of gut samples for analysis

The samples were divided according to sex, age and month collected. Samples from each category were then pooled and placed in a nylon mesh bag (the lower section of pantyhose) which was in turn placed in a water bath at a constant temperature of 25^{0}C. The bags were rinsed daily and the water replaced until it remained clear after 24 hours soaking. The cuticles were then considered transparent enough for identification. Ten to 14 days were required to clear a sample to this stage. The cleared samples were sieved using 1400um, 710um and 300um aperture sieves and the material remaining on the 300um sieve collected and stored in 15% formalin. Material from the other sieves, ie. 1400um and 710um, was discarded after noting the presence of seeds or undigested berries, as the main purpose of these sieves was to remove larger particles and to quicken the sieving process.

3.2.3 Analysis of gut samples

After stirring to ensure homogeneity a small quantity (enough to cover a microscope slide with a thin layer, ie. about 0.25cc) of material was taken from each sieved sample, placed on a glass slide and covered with a cover slip. This preparation was then examined under 100x magnification. Fifty identifications were made per slide until a total of 250 identifications had been made for each sample. This number of identifications was found to be the optimal for accuracy by

Stevens (1977). Homolka (1987) found that it was sufficient to examine 50 to 100 microscope fields at 100x magnification to record even those food items which were present in small quantities. The slides were examined using standard transects as this method is considered the most accurate (Nugent 1983). Results were then converted to percent frequency of occurrence to allow comparison between and within months and seasons. Contingency table analysis was completed using a computer package.

3.2.4 Preparation of reference slides

In order to identify the gut contents several slides were made for the more common plant species in the grassland. The method adopted to prepare these slides was that used by Joy Talbot (Centre for Resource Management) as it was found to be much more controllable and usable than that used by earlier researchers (eg. Fitzgerald 1976, Flinders and Hansen 1972) which tends to rely on strong acids and chemicals and very often completely destroys the more fragile cuticles such as those of *Trifolium* spp.

The method used in this study was as follows:

1. Transverse sections (2-3 cm) of leaves, stems, etc. were cut and one edge removed so that the section could open during maceration. These preparations were fixed in FAA (appendix 1). Sections may be stored in this solution.

2. Fixed sections were placed in 50% nitric acid in small capped and labeled bottles and allowed to macerate until air bubbles appeared between the surfaces (this took up to three days).

3. The acid was removed, the solution washed and covered with 20% ammonium hydroxide for an hour. Sections can be stored in this solution also.

4. After removing the ammonium hydroxide the sections were rinsed in 15%, 30% then 50% alcohol for ten minutes to one hour depending on the size of the sample. Safranin was added to the 30% alcohol to stain the mesophyll (2-3 hours).

5. Stained samples were placed on a slide, opened out flat and the stained mesophyll removed using a fine brush. This was done under a dissecting microscope and can take an hour per species. Great was taken at this stage as it is very easy to tear cuticles and therefore destroy the sample.

6. If maceration was satisfactory the sample was covered in 50% alcohol and Delafields haematoxylin to stain the cuticle and left for 24 hours.

7. The alcohol series was carried on to 100%.

8 The dehydrated sample was then placed in xylene until the alcohol was replaced (15-30 seconds) and then floated

onto a slide so that any microhairs on the cuticle were against the cover slip. Any excess solvent was then mopped up before adding the mounting medium (permount) and a coverslip.

The slides made from material from the study area were then used in conjunction with photomicrographs.

When preparing a reference collection it must be noted that plants of the same species from different regions may have different cellular characteristics and also that stems, leaves, sheaths etc. all have different cell patterns and therefore each requires a reference slide.

3.3 Calorimetry

Samples of the five main dietary items were collected from the study area each month. Only the five main dietary items were analysed because these varied from contributing over 50% to under 10% of the total diet and this magnitude of difference was considered to be sufficiently large to explain any preference patterns shown by the hares. The plant samples were sorted and any species other than the one required were removed to give as pure a sample as possible. The five plant types measured were Festuca novae-zelandiae, Poa colensoi, Hieracium pilosella, the combined grasses (Anthoxanthum odoratum, Holcus lanatus, Agrostis tenuis) and Rhacomitrium lanuginosum. All samples were placed in a drying oven at $60^{0}C$

for five days after which time they were considered sufficiently dry to use in the calorimeter. A small quantity (usually about 0.7g) of the dried sample was placed into a calorimeter crucible. The sample weight was noted in grams to four decimal places. The crucible was placed in the calorimeter, the bomb screwed on and filled with oxygen to about 22atm. After firing the maximum reading was noted, the bomb dismantled and the crucible reweighed to determine the amount of material remaining uncombusted. This figure was then subtracted from the initial sample weight and the calorific value calculated from the corrected weight.

The calorific value was calculated as follows,

$$kcal/g = (O_3-O_1)y/z$$

where

O_3 = Reading from combustion of sample.

O_1 = Constant reading due to combustion of fuse.

y = Calibration constant. Found by combusting a known amount of a known calorific content sample. Benzoic acid was used in this case.

z = Weight of sample in grams.

Analysis of variance of the results was completed using a computer package.

3.4 Neutral detergent fibre analysis

Digestibility of the various plant species was determined using a modified version of the Van Soest method (Van Soest 1967, Van Soest and Wine 1967). This method is a neutral detergent process with further digestion by acid detergent and sulphuric acid following the steps indicated in figure 3.1 (Schemnitz 1980). However, Servello et al (1983) and Nagy and Haufler (1980) have shown that the cell solubles (CS) released by the neutral detergent process are 98% digestible and are highly correlated (r=.90) with the digestible dry matter. In cases such as this study where a ranking rather than an actual figure for digestibility is required it may not be necessary to proceed past the neutral detergent process to obtain a useful measure (D. Poppi pers com.). The principle of the process is to separate the fibrous material in the cell from the non-fibrous (or soluble) fraction. The neutral detergent solution essentially ruptures the cell wall, causing the cell contents or cell solubles to be released and allowing the two fractions to be seperated.

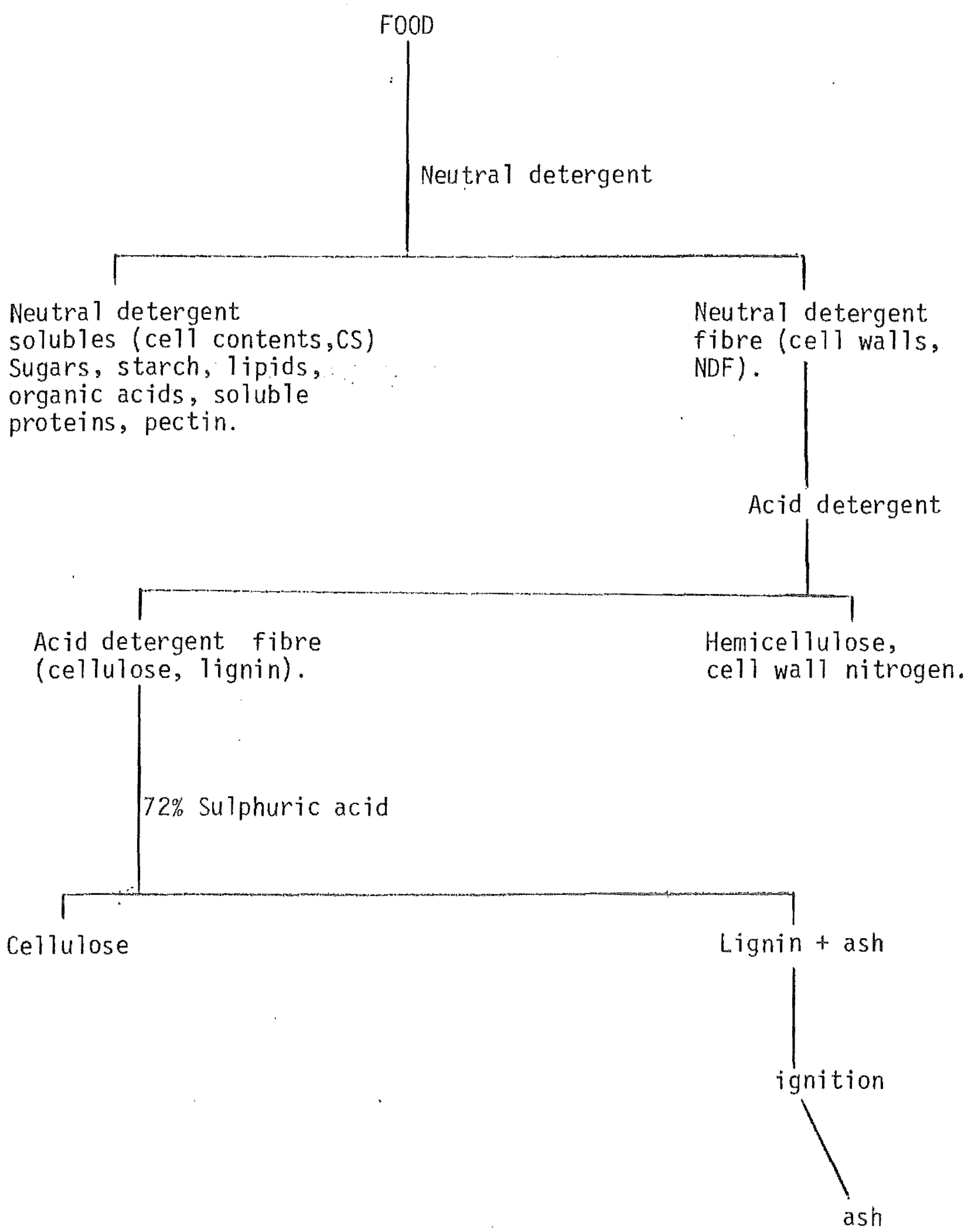


Figure 3.1: Flow chart of the Van Soest method of fibre or digestibility determination.

The process used a refluxing apparatus with a heating mantle, 250ml beakers and condensers of 250ml round bottom flasks, with a supply of cool water. The samples were dried and ground through a 1mm mesh sieve. Two sub-samples were weighed to four decimal places and placed into duplicate 250ml beakers. A control sample with a known percentage fibre was included to check the reproducibility of the method. Sixty mls of neutral detergent fibre (NDF) reagent (see appendix 2) was added to each beaker. The refluxing apparatus was assembled by placing the beaker containing the solution on the heating mantle and the round bottom flask with the water supply on top of this.

The water was turned on and the sample heated to boiling in 5-10 minutes. The heat was reduced as boiling began to avoid foaming and the sample simmered for one hour. The sample was then cooled with water running through the condenser flasks, filtered through glass wool and washed with hot distilled water. The water in the sample was removed with a double rinsing of acetone and the acetone evaporated in a fume cupboard before drying overnight at 105^0C. Next day the crucibles were weighed when cool. The samples were then ashed in a muffle furnace at 500^0C for five hours and reweighed when cool.

Ash free NDF was calculated using the following equation:

$$\%NDF = \frac{\text{(wgt of cruc + fibre)} - \text{(wgt of cruc + ash)}}{\text{DM. wgt of sample}} \times 100$$

Statistical analysis of the results was completed using analysis of variance and a computer package.

3.5 Secondary metabolite analysis

3.5.1 Extraction of secondary metabolites

Secondary metabolites were extracted from fresh plant material from the study site. The material was mashed using a mortar and pestle, methanol added and the solution put in a stoppered vial. The methanol was removed after 24hrs and replaced with fresh methanol. This was repeated four times to ensure maximum removal of the secondary metabolites as suggested by Ribereau-Gayon (1972). The solution with the extract was then placed in a common container and allowed to evaporate. When evaporation was completed, leaving a concentrated fluid, the material was centrifuged to remove particulate matter and the cleared fluid stored in a stoppered vial until needed.

3.5.2 Analysis of secondary metabolites

Folin-Denis reaction

Total phenolics were measured using the Folin-Denis method. This reagent consists of a mixture of phosphotungstic

($H_3PW_{12}O_{40}$) and phosphomolybdic ($H_3PMo_{12}O_{40}$) acids, which is reduced, concomitantly with the oxidation of the phenols, to a mixture of the blue oxides of tungsten (W_8O_{23}) and molybdenum (Mo_8O_{23}). The reagent was prepared by mixing 750ml of water, 100g of $Na_2WO_4,2H_2O$, 20g of phosphomolybdic acid and 50ml of phosphoric acid. This mixture was boiled under reflux for two hours and, after cooling, made up to one litre (Ribereau-Gayon 1972).

A solution of sodium carbonate was also prepared by dissolving, at 70-80^{o}C, 35g of anhydrous Na_2CO_3 in 100ml of water. After cooling overnight, the supersaturated solution was seeded with a crystal of $Na_2CO_3.10H_2O$, and after crystallisation was filtered through glass wool.

The analysis was performed by taking a sample containing approximately 1.0mg of phenolic substances and placing it in a 100ml flask containing about 75ml of water, 5ml of the Folin-Denis reagent and 10ml of the Na_2CO_3 solution. The volume was made up to 100mls. After shaking, the absorbance was measured at 750nm in a 1cm cell. The results are expressed as absorbtivities (Ribereau-Gayon 1972).

<u>Vanillin reaction</u>

The total amount of monomeric tannins was determined using the vanillin reaction (Goldstein and Swain 1963). Four mls of a freshly prepared solution of 1% vanillin in 70% conc. sulpuric acid was added to two test tubes, one containing the solution to be analysed (with not more than 0.1ml methanol present) and made up to 2ml with water, and the other containing 2ml of distilled water only. Another two test tubes were prepared as above but instead of the vanillin solution being added, 4ml of 70% sulphuric acid was added. Absorbtivities were measured at 500nm in 1cm cells using the tube containing water and acid only as the blank. The vanillin value, V, was found by using the equation $A_1-(A_2+A_3)$ where A_1 is the absorbtivity of tube 1 (test + reagent), A_2 of tube 2 (water + reagent) and A_3 of tube 3(Test + acid).

Leucoanthocyanidin reaction

The total amount of condensed tannins was determined using the leucoanthocyanidin reaction. There are two methods of carrying out this reaction; either in aqueous or alchoholic solution. The latter was used in this case as it gives a better yield of anthocyanidin (Ribereau-Gayon 1972).

The method followed was that of Swain and Hillis (1959) (from Ribereau-Gayon 1972) where 1ml of the solution to be analysed (which did not contain more than 50% methanol or ethanol) was added to each of two tubes closed by a glass stopper. Ten mls of 5% conc. HCl in n-butanol was added to each tube and the contents mixed. One tube was heated at $100^{o}C$ for exactly 40mins, the stopper being firmly closed after 4mins, cooled in running cold water for 4mins and the difference in absorbtivity between the two tubes measured at 550nm in a 1cm cell.

3.6 Vegetation sampling

3.6.1 Availability

Ninety-five 0.5m x 0.5m quadrats in the study area were examined each month throughout the year. These quadrats were located at five metre intervals along two transects bisecting the river flat. They were repeated in the same place each month to allow for any discrepancies occurring in the grasslands due to irregular distribution of plant species.

For each plant species presence or absence and approximate ground cover as estimated by one of six Braun-Blanquet cover classes were recorded. It was considered that this method would give the most accurate result feasible in relation to logistic problems, such as time available (A. Rose pers. comm.).

The Braun-Blanquet cover classes used were as follows:

1 = <1%

2 = 1-5%

3 = 6-25%

4 = 26-50%

5 = 51-75%

6 = 76-100%

In addition to this an estimation of the ground cover to the nearest five percent of the five main species in the grassland was done every two months of the year (January, March, May, July, September, November). This method gave no estimate of total plant availability because it did not measure the total biomass of each species. However, it was cosidered to be the only method that would satisfactorily give results comparable with the diet results. Any estimation of biomass would be very approximate only and as most plants present on the study site were flat growing this method gave reasonably reliable results.

Statistical analysis of the results was completed using Spearman rank correlations on a computer package.

3.6.2 Exclosure plots

To measure potential additional grassland growth in the absence of hares twelve 1.4m x 1.4m exclosure plots were set up on the predominant vegetation association of the riverflat ie. the moss (Rhacomitrium lanuginosum)/ (Hieracium pilosella)/ (Festuca novae-zelandiae) association. These plots consisted of four 25mm x 25mm wooden stakes surrounded by 600mm high wire netting (mesh size 50mm). The use of wire mesh allowed smaller invertebrate grazers to utilize the area enclosed in the normal way and did not disturb environmental conditions inside the exclosure. It is unlikely that hares would have been able to jump into the plots or that they would even try to, nor could they lift the wire netting which was pegged to the ground. No hares were seen, and no fresh faecal pellets were found, inside the plots so it is assumed that the exclosures were effective.

The exclosure plots were put in place at the beginning of one growing season, August 1988. Measurements were taken at the end of that season (April 1988) and also at the beginning of the next season (September 1988). Six plots were measured each time. A 300mm x 300mm area was dug up inside the exclosure and a similar area outside the exclosure. The vegetative cover of these sections was removed at ground level, dried and weighed. A comparison was made between sections taken from inside the exclosures and those from outside. Any differences between the two averaged figures could then be attributed to the hares.

This type of experiment is well known to be difficult to gain significant results from even on a very uniform grassland. As this grassland was very variable and also because of the very limited number of plots examined, results from this experiment will be interpreted with appropriate caution but the results may be useful in indicating some broad trends.

Chapter 4: Results

4.1 Diet

Hieracium pilosella was the most common item in the hares diet in all months (Fig 4.1). On an averaged seasonal basis (Fig 4.2) grasses were the second most common with the tussocks next most common. *Rhacomitrium lanuginosum* was the least favoured. On a seasonal basis this pattern of preference was consistent throughout the year (Fig 4.2). Plants categorised as 'others' contributed a significant proportion to the diet, but as this is a grouping of many (13) and varied species it has not been emphasised in the overall analysis as much as individual species or groups of similar species, such as the grasses.

The highest level of *Hieracium* in the diet was 50% for adult females during May (Fig 4.5) and the lowest 24% for adult males during April (Fig 4.6). The consumption of *Hieracium* varied from month to month (Fig 4.1), but all age and sex classes showed a maximum consumption during May (Figs 4.4-4.6). Adults also showed a secondary increase in consumption during November (Figs 4.5 & 4.6). These two maxima coincided with a general decrease in consumption of other food categories during the same period. Averaging the monthly results to obtain seasonal values tended to flatten the fluctuations in the monthly data and allowed trends to be more easily seen. On a seasonal basis (Fig 4.2) (Spring (September, October, November), Summer (December, January, February), Autumn (March, April, May), Winter (June, July, August)) Hieracium made up an average of 32.3% of the diet. Fig 4.2 indicates a relatively constant intake of Hieracium over the year, with a slightly lower consumption during summer.

The next most common food category were the grasses, which showed a maximum intake during the March to May period for juveniles (Figs 4.3 & 4.4) and during the July to October period for adults (Figs 4.5 & 4.6). Adults also had a slight increase in consumption during the March to May period. The different species of grasses were eaten in different orders of preference by adults and juveniles. Adults preferred Anthoxanthum odoratum with peak consumption occurring during spring (PFO=16.6). Agrostis tenuis was the second most preferred grass with percent frequencies of occurrence between 4.3 and 9.8 and with maximum consumption during autumn for both females and males. Holcus lanatus varied between the sexes in the season of maximum consumption. Adult females ate most Holcus during summer and adult males during winter. Minimum PFO was 1.0 and maximum 3.8. Juveniles preferred A. tenuis (max. PFO 11.2, min. PFO 4.4). Consumption of this grass reached a maximum during the autumn/winter period for juveniles. A. odoratum was the next most commonly eaten grass by juveniles with PFO's between 5.8 and 14.0, and intake again at its maximum during autumn. H. lanatus was the least commonly eaten grass with PFO's between 0.8 and 8.0. Male and female juveniles appeared to prefer this grass during different seasons with the males maximum percent intake during summer and females during autumn. Juvenile males consumed greater quantities of H. lanatus than did juvenile females. The average intake of grasses was 20.9 with a minimum of 10.2 and a maximum of 27.0% (Figs 4.1 & 4.2).

Consumption of tussocks showed a similar pattern for all age and sex classes with a general maximum during the December to March period and minimum during the May to September period (Figs 4.3-4.6). The two tussock species present in the gut samples were F. novae-zelandiae and P. colensoi. Of these two species the most commonly eaten was Festuca with PFO's ranging from 2.6 to 16.2. Consumption of both tussocks was maximum during summer for all sex/age classes (Figs 4.7-4.10).

Rhacomitrium lanuginosum consumption was maximum for all age/sex classes during June with minimum consumption occurring during the December-January and March-May periods. This moss appeared to be a relatively unfavoured food item and made up only 3.2 to 10.6% of the total diet. Peak consumption of Rhacomitrium occurred during winter (especially June and August) (Fig 4.1) with adult males also eating larger amounts during summer (Fig 4.10).

Plants listed under others varied in consumption between sex and age classes. Juveniles consumed more of these plants during January, February and March and adults during June, July and August (Figs 4.3-4.6). This group contained 13 species (table 4.1), none of which individually exceeded 13% of the total intke. Most species individually made up between 2 and 7% of the total gut contents. Overall consumption of

Table 4.1: Percent frequency of occurrence for species listed under 'others.

Juvenile female

Species	Spring	Summer	Autumn	Winter
Carex coriacea	–	4.9	4.9	0.9
Moss	–	4.5	4.0	4.6
Trifolium spp.	–	2.4	2.5	0.8
Carmichaelia spp.	–	1.4	4.2	11.6
Corokia cotoneaster	–	3.2	0.4	0.0
Rumex acetosella	–	1.4	1.8	0.0
Hypochaeris radicata	–	0.6	0.6	0.3
Digitalis purpurea	–	0.4	0.7	1.0
Luzula crinita	–	0.1	0.0	0.1
unknown	–	4.0	3.2	4.4

Juvenile male

Species	Spring	Summer	Autumn	Winter
Carex coriacea	–	5.7	3.4	3.2
Moss	–	4.3	5.4	2.4
Trifolium spp.	–	3.3	2.8	0.0
Carmichealia spp.	–	7.1	4.8	9.3
Corokia cotoneaster	–	1.7	1.4	4.8
Rumex acetosella	–	1.8	0.7	0.4
Hypochaeris radicata	–	1.0	0.7	1.2
Digitalis pupurea	–	1.6	0.7	0.0
Luzula crinita	–	0.3	0.0	0.0
Schoenus pauciflorus	–	0.3	0.0	0.0
Taraxicum officianale	–	0.2	0.0	0.0
Unknown	–	3.3	2.4	3.6

Table 4.1: Continued.

Adult female

Species	Spring	Summer	Autumn	Winter
Carex coriacea	1.8	3.9	4.3	3.8
Moss	3.4	4.8	3.9	3.0
Trifolium spp.	3.7	2.4	1.4	0.9
Carmichealia spp.	3.1	2.7	4.2	12.2
Corokia cotoneaster	0.3	0.4	0.9	1.0
Rumex acetosella	0.8	2.9	1.0	0.6
Hypochaeris radicata	1.7	0.5	0.0	0.7
Digitalis purpurea	0.4	0.4	0.9	0.7
Luzula crinita	0.0	0.2	0.0	0.7
Juncus effusus	0.3	0.0	0.4	0.0
Insect cuticle	0.0	0.2	0.0	0.0
Unknown	2.4	3.2	1.7	1.6

Adult male

Species	Spring	Summer	Autumn	Winter
Carex coriacea	1.8	5.9	2.8	4.8
Moss	3.0	2.9	3.4	4.0
Trifolium spp.	3.5	6.6	2.0	1.5
Carmichealia spp.	1.0	1.2	8.8	7.8
Corokia cotoneaster	1.2	1.3	2.4	2.6
Rumex acetosella	0.4	3.5	0.5	0.4
Hypochaeris radicata	1.9	1.0	0.7	1.4
Digitalis purpurea	1.1	1.6	0.7	0.9
Epilobium melanocaulon	0.4	0.5	0.0	0.0
Schoenus pauciflorus	0.4	0.0	0.0	0.0
Unknown	2.4	3.3	2.4	2.8

species in this group remained relatively constant throughout the year but individual species did tend to vary. For example, the Carmichaelia species (C. monroi and C. longiflorum) were consumed in relatively large quantities during winter (and autumn by adult males) (PFO 7.8-12.2) but during summer and spring they were hardly eaten at all (PFO 1.0-7.1). The swampgrass Carex coriacea was eaten in consistent quantities throughout the year (usually about 2-3%). Other species in this group are eaten in very low quantities or infrequently. The most consistent species of these was Hypochaeris radicata which was typically consumed at a PFO of 0.5 to 1.5.

Rosehip berry seeds were noted in all sieved gut samples from February to May.

Those plant cuticle fragments unable to be identified (labelled as unknown in table 4.1) consistantly made up from 3 to 4% of the gut sample, although some samples yielded an unknown PFO of below 2%.

Insect cuticle was found only once, in an adult female sample during summer and rosehip (Rosa rubiginosa) berries were present in all gut samples from February to May, but the amount was unable to be determined.

In summary H. pilosella was the plant species consumed in the greatest quantities. Grasses were eaten next most frequently and tussocks ranked as the third most commonly eaten food type, although there was little difference between these two. Another 13 species made up the greater portion of the remaining diet, with R. lanuginosum ranking as the fifth most preferred category (Fig 4.1).

Statistical analysis of the data has revealed some interesting trends. Contingency table analysis of the diet data to determine any difference between sex, age and season showed that diet varied significantly between the sexes (X^2_4=0.297, P<0.01). The diet of adults varied significantly between seasons (X^2_7=1.239, P<0.01) as did the diet of juveniles (X^2_5= 0.5543, P<0.01). Adult and juvenile diets were also significantly different from each other during summer (X^2_{60}= 37.48, P<0.01) but were not significantly different during autumn (X^2_{50}= 29.70, P<0.01) or winter (X^2_{40}=22.16, P<0.01) indicating that juvenile diet becomes more similar to adult diet as juveniles age. This conclusion was reinforced by a significant interaction effect between age and season during contingency table analysis.

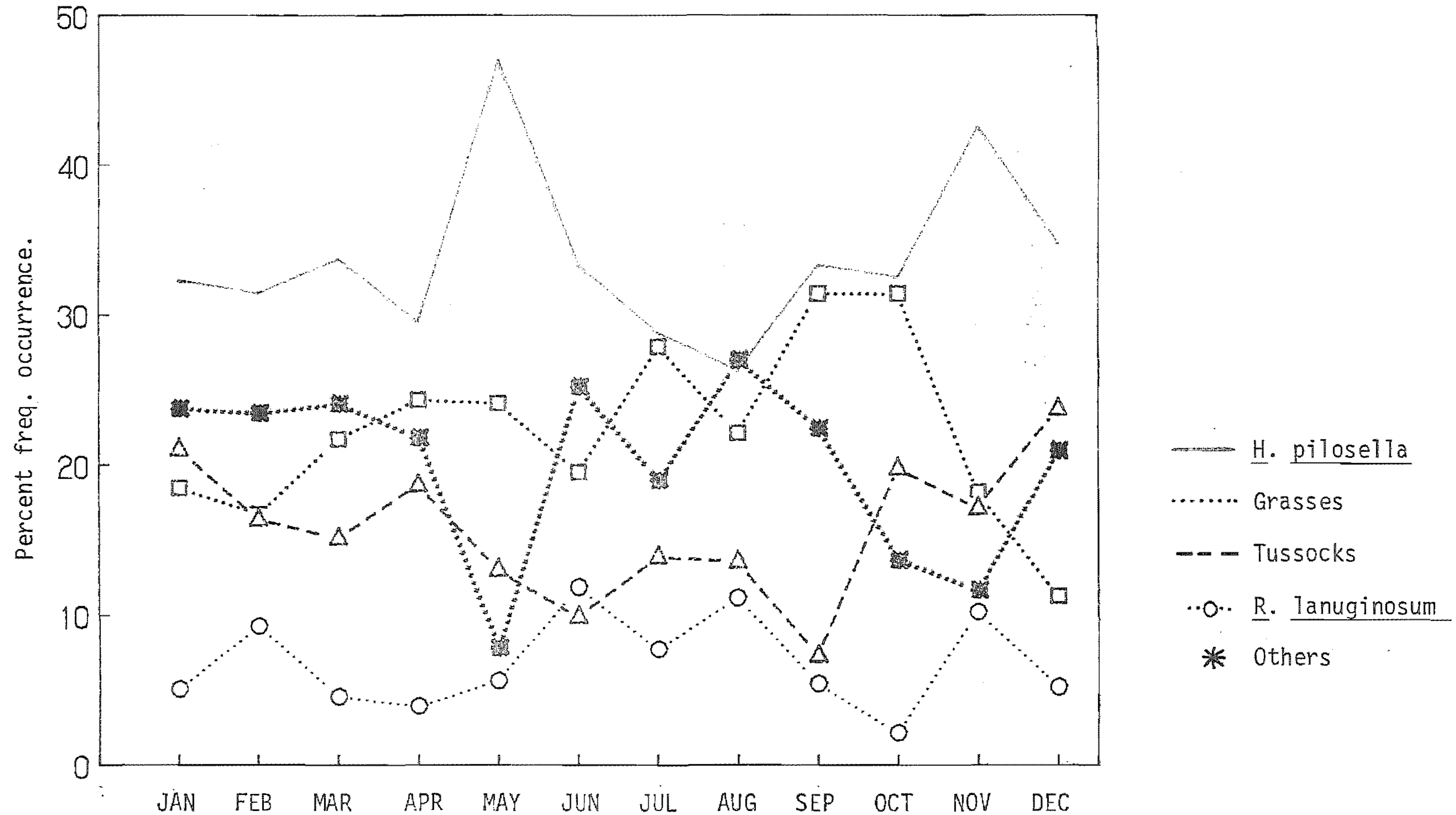


Figure 4.1: Monthly diet of the hare population in the study area.

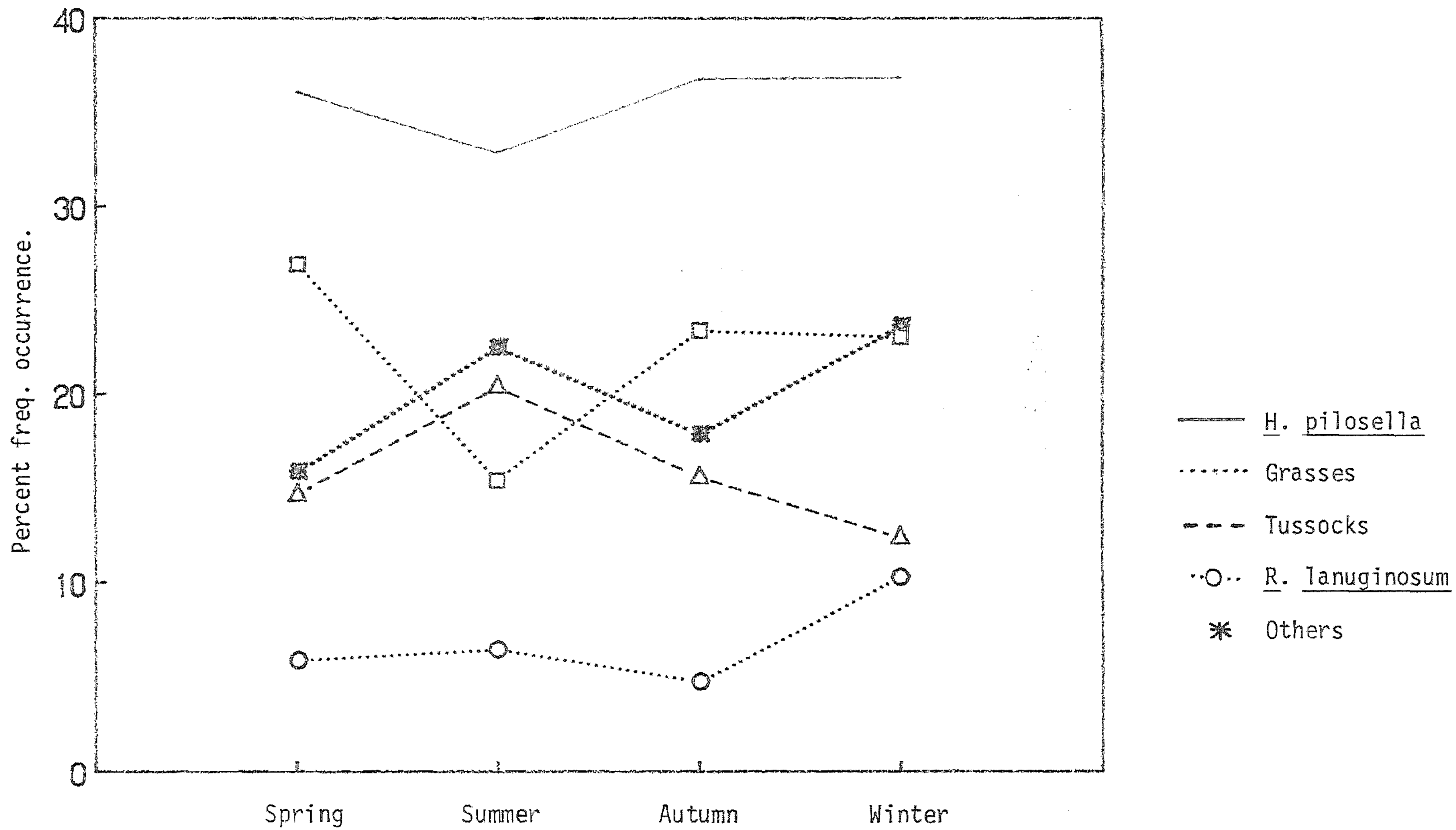


Figure 4.2: Seasonal diet of the hare population in the study area.

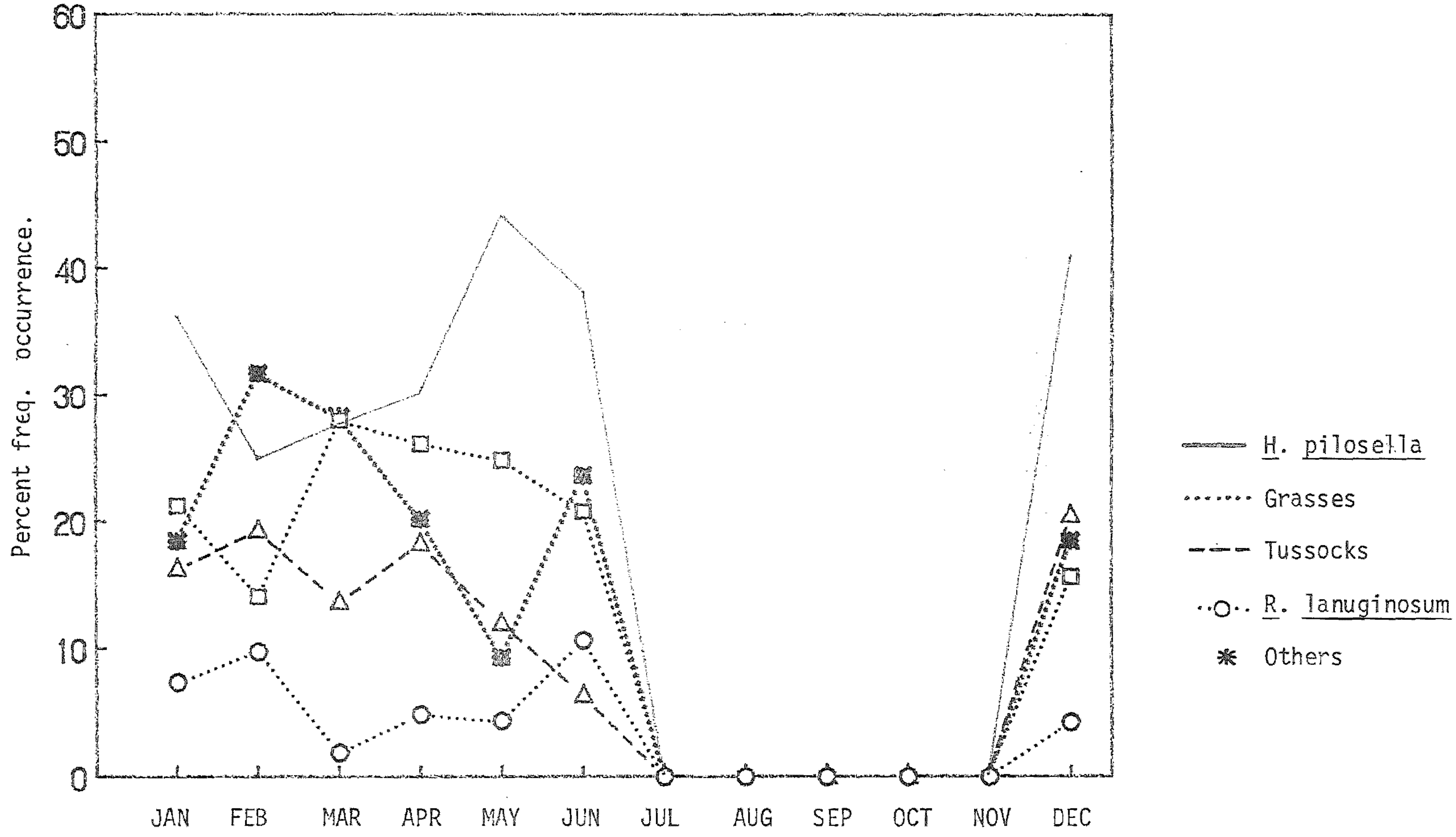
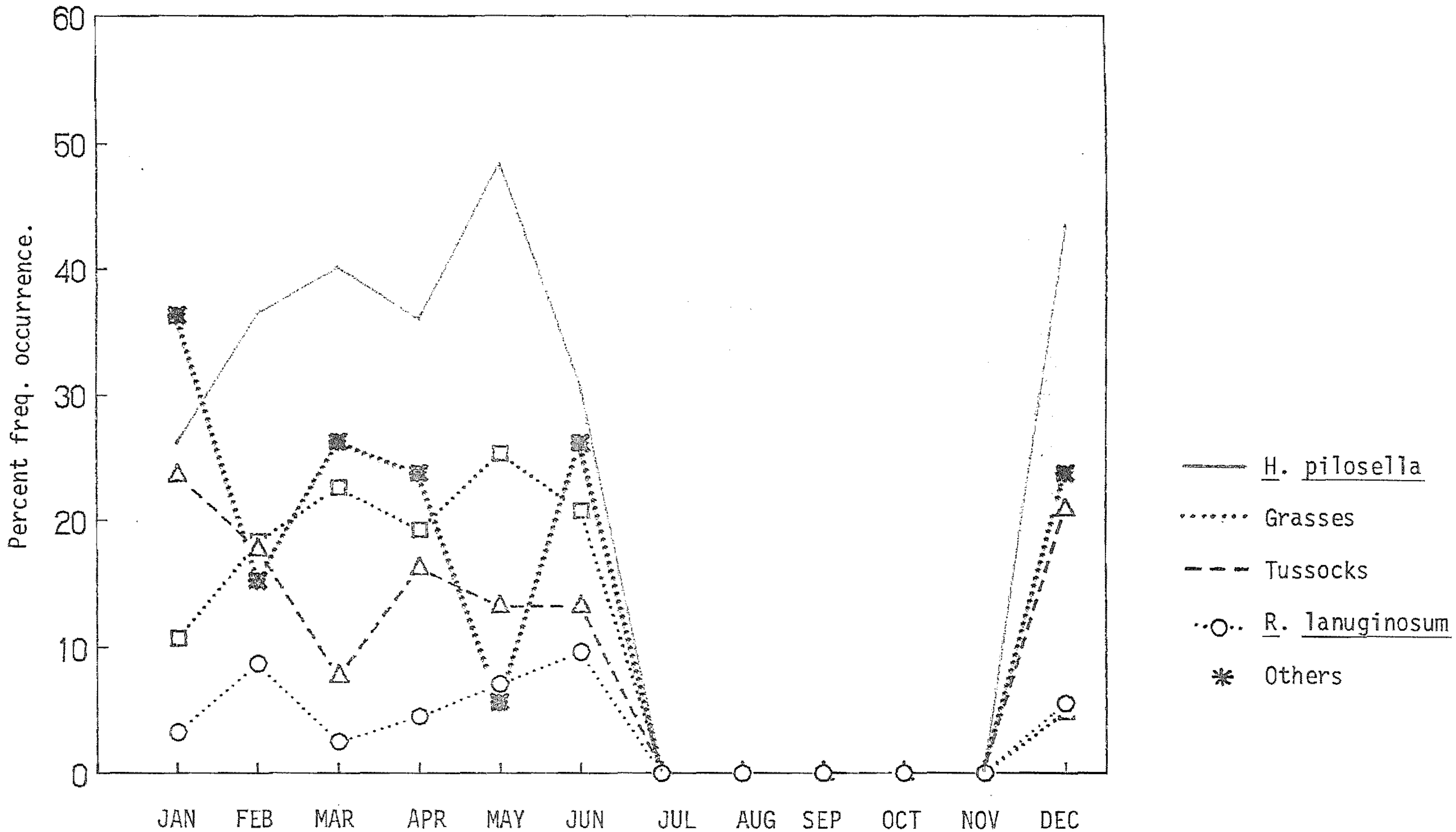


Figure 4.3: Monthly diet of juvenile female hares.



<u>Figure 4.4</u>: Monthly diet of juvenile male hares.

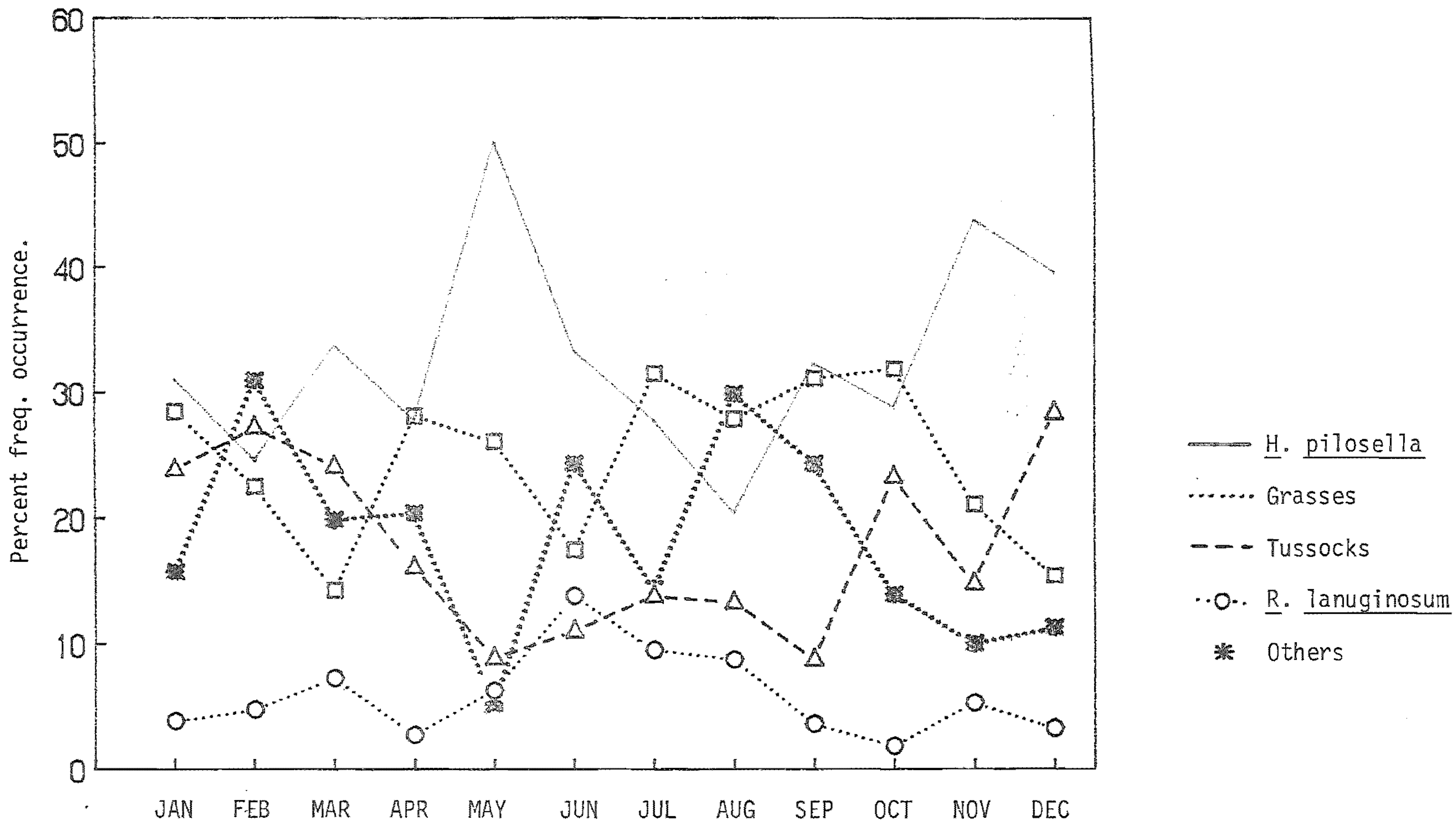


Figure 4.5: Monthly diet of adult female hares.

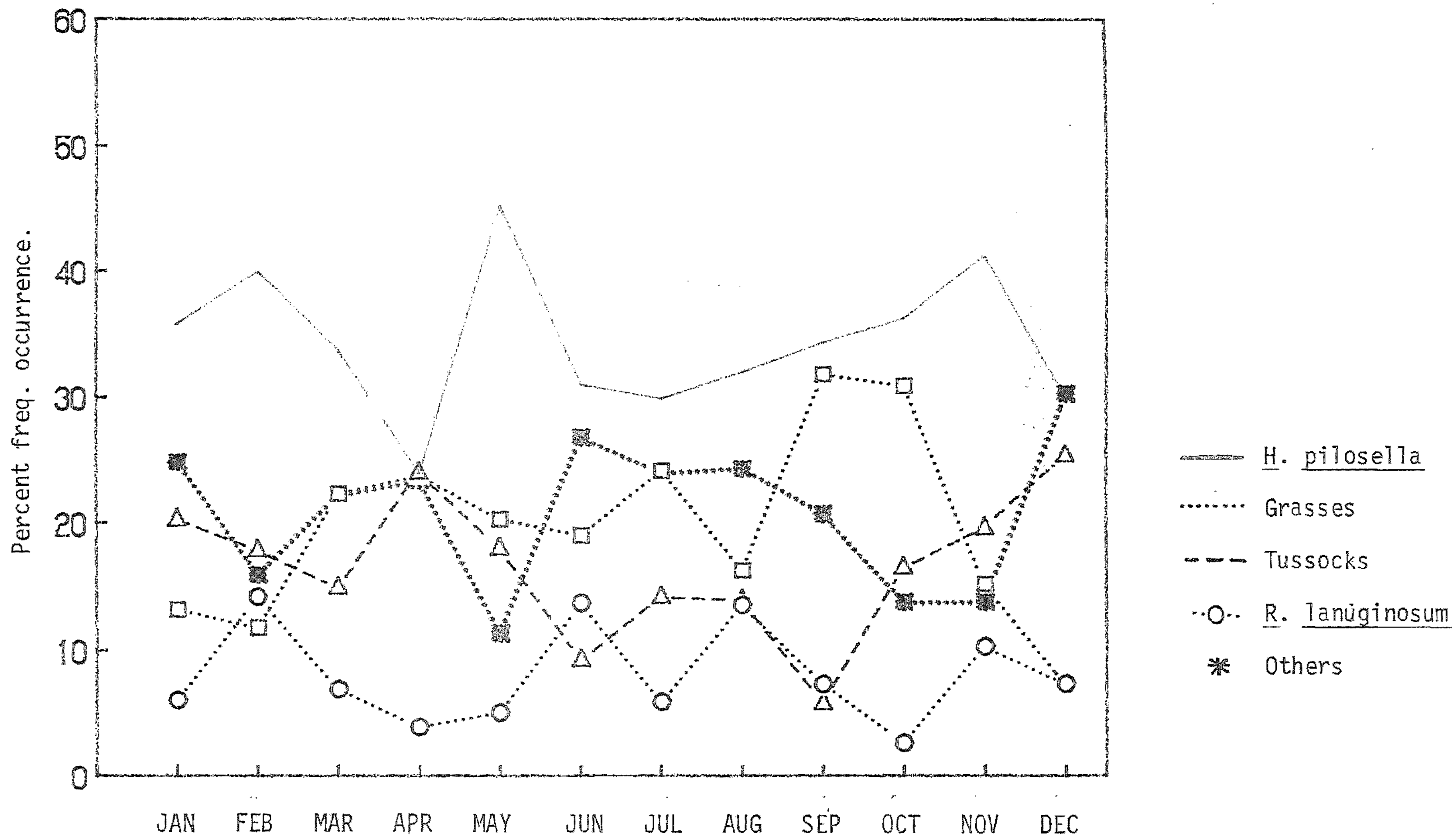


Figure 4.6: Monthly diet of adult male hares.

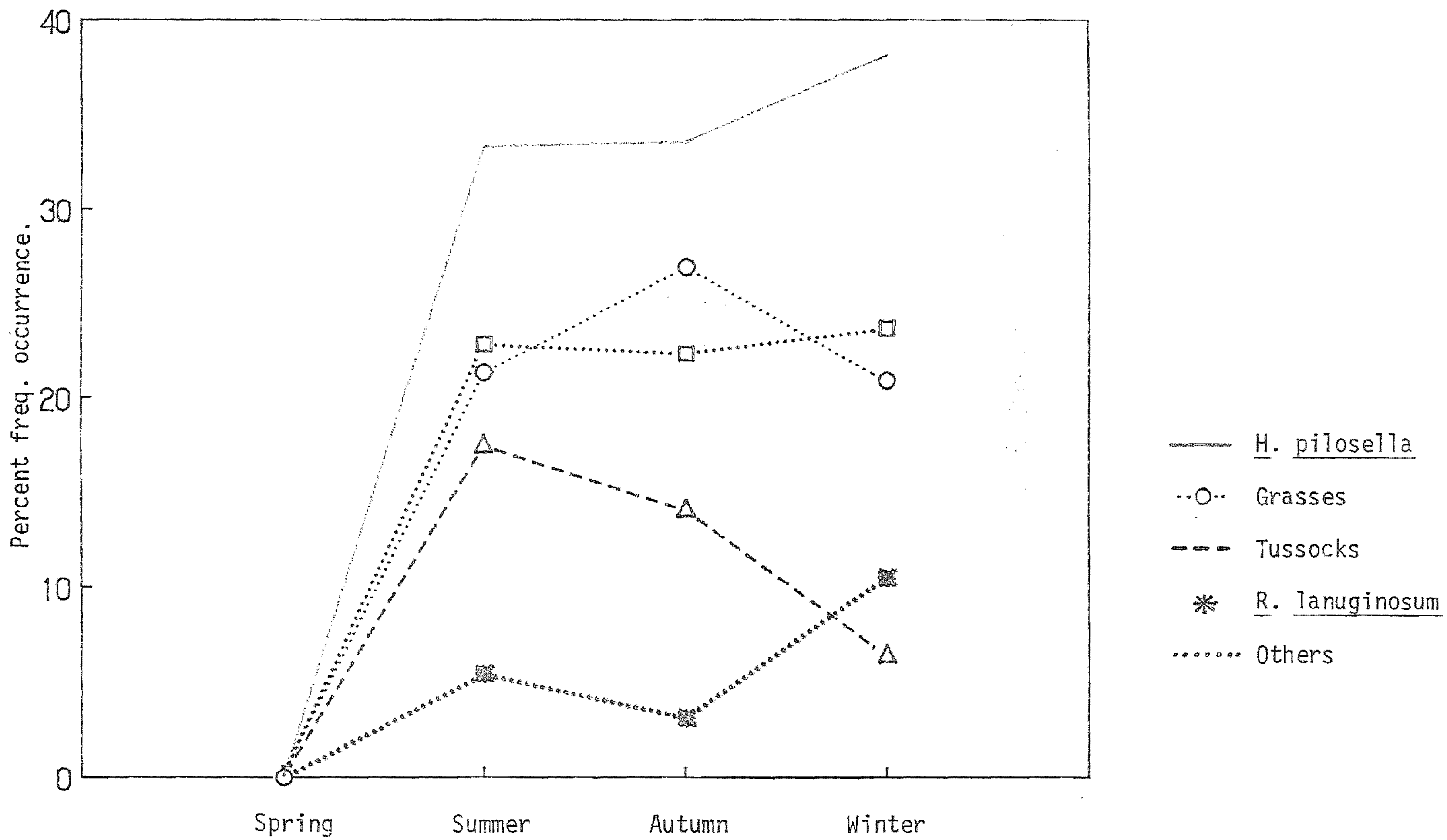


Figure 4.7: Seasonal diet of juvenile female hares.

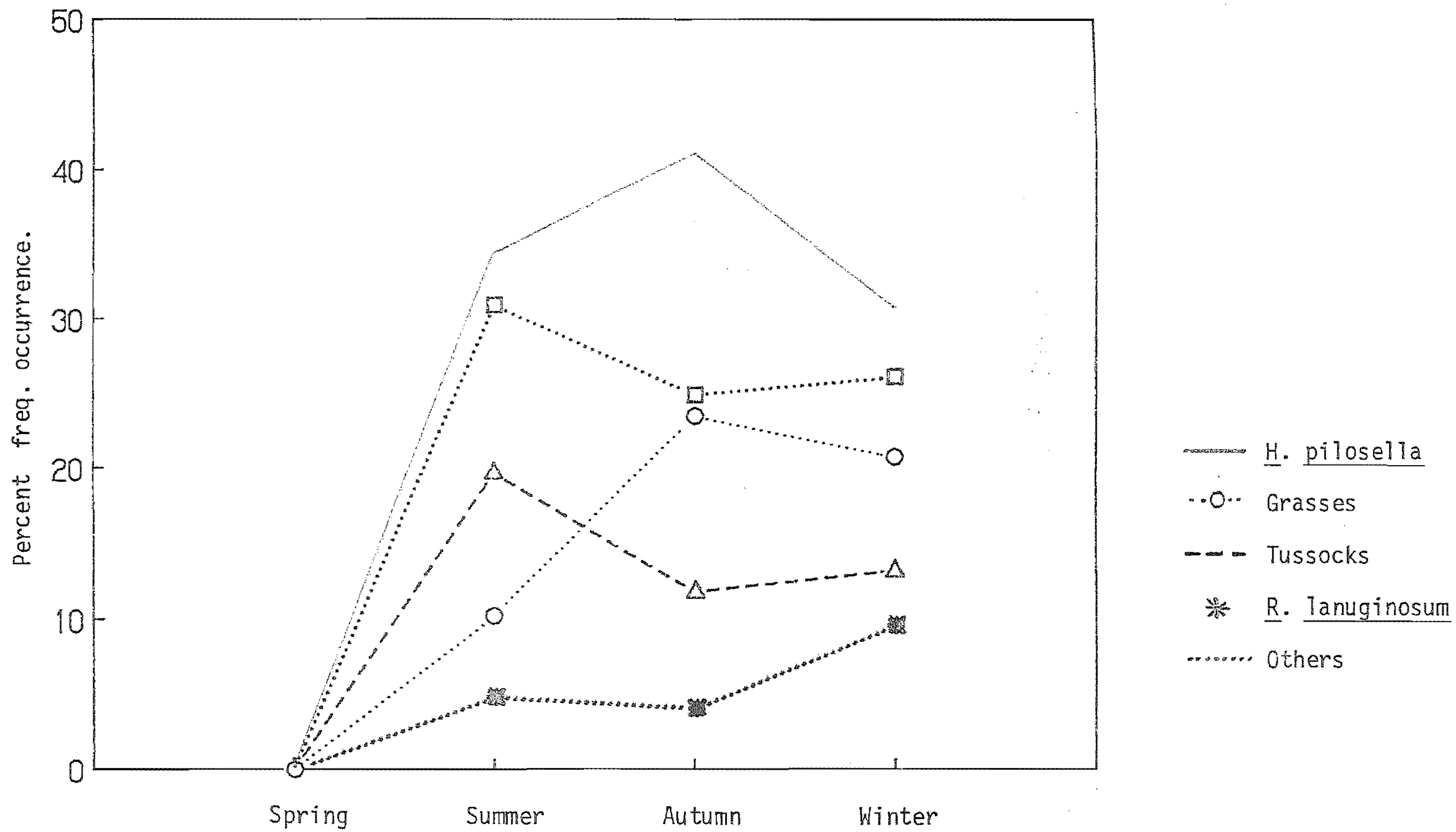


Figure 4.8: Seasonal diet of juvenile male hares.

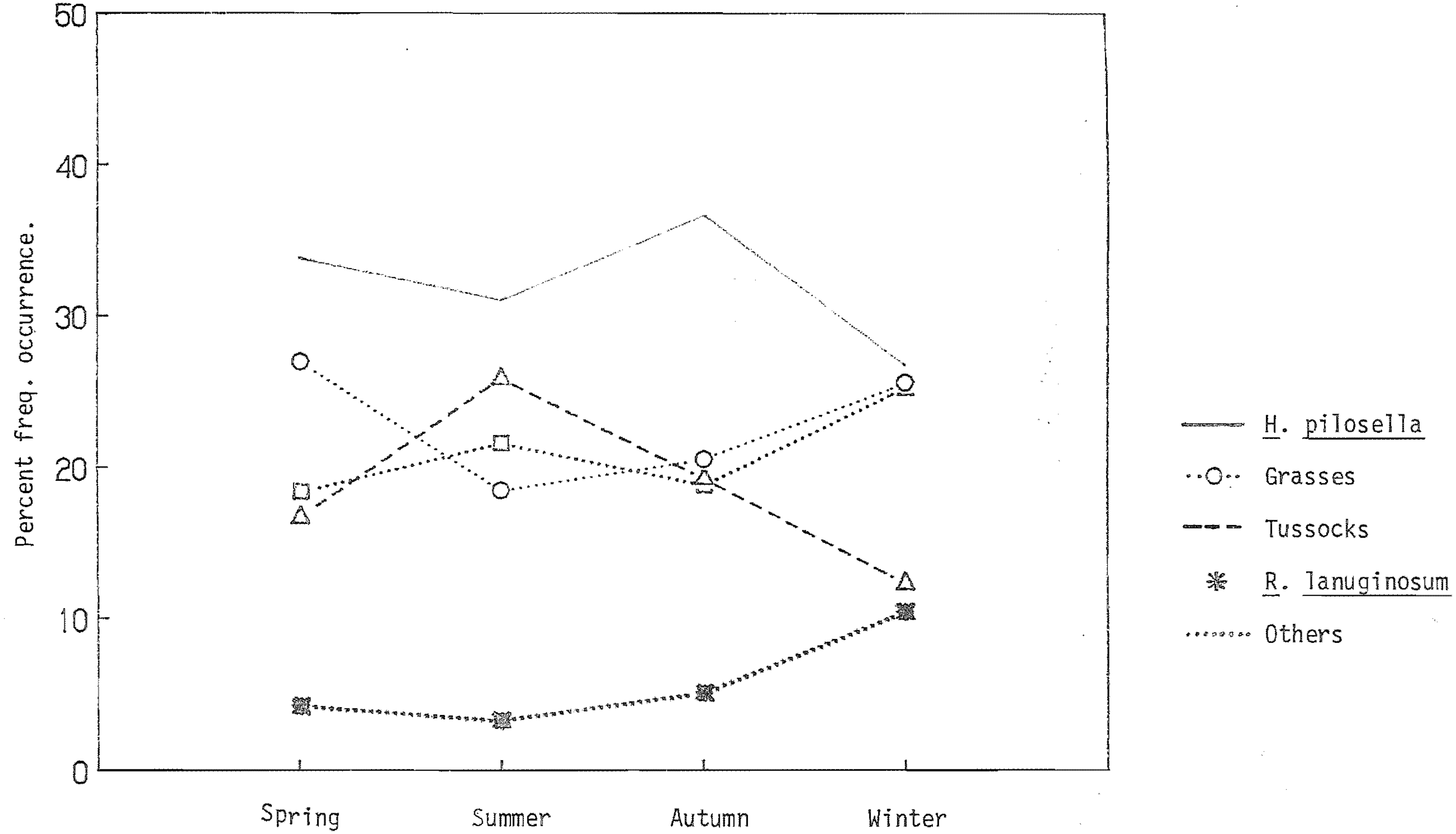


Figure 4.9: Seasonal diet of adult female hares.

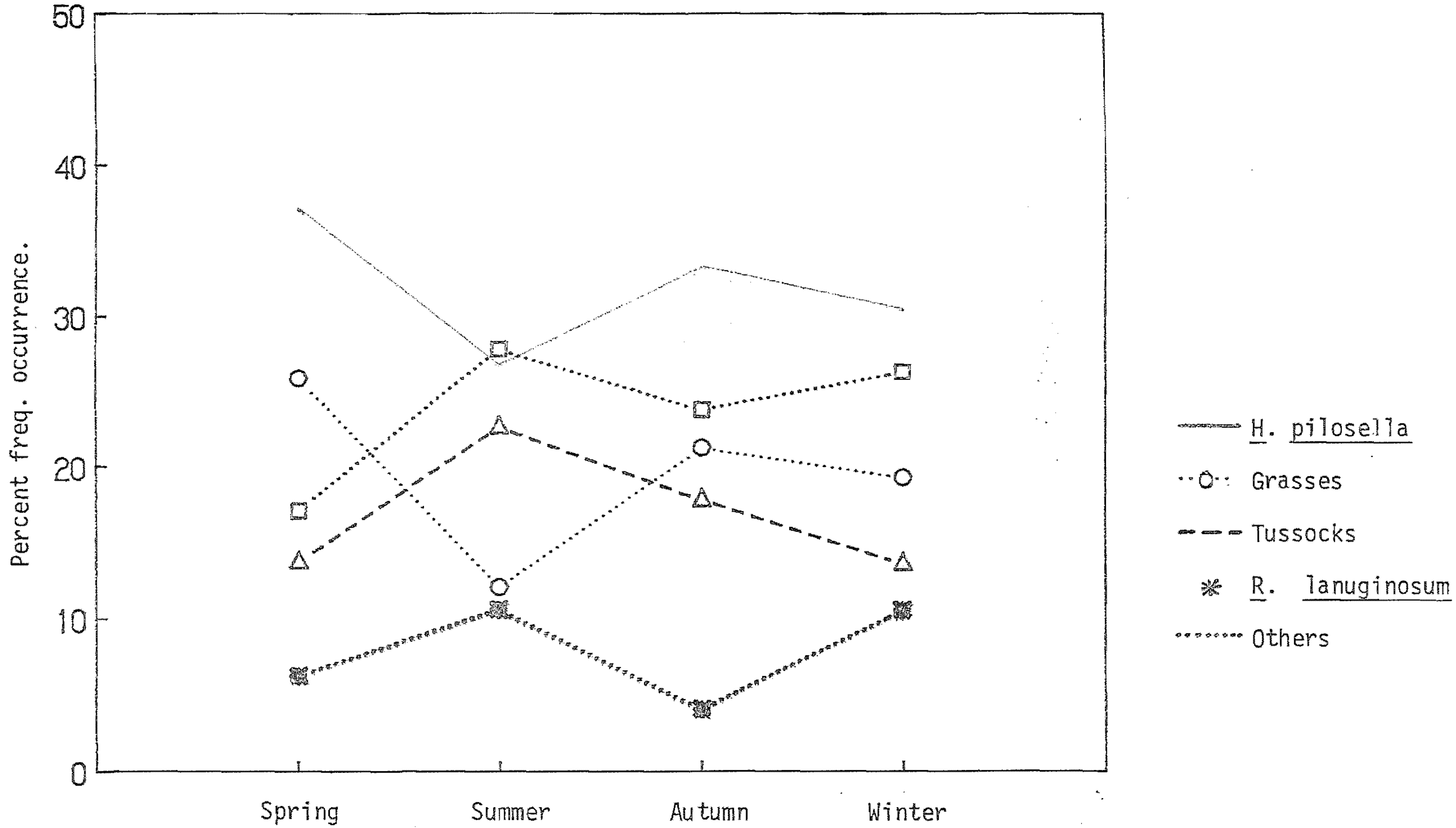


Figure 4.10: Seasonal diet of adult male hares.

4.2 Vegetation sampling

4.2.1 Availability

The results of the monthly vegetation sampling are presented in fig. 4.11 and a seasonal presentation of the data, more useful in showing trends, in fig.4.12. Rhacomitrium lanuginosum had three distinct months of minimum ground cover during April (51%), September (49%), and December (45%), but otherwise the percentage ground cover remained reasonably constant. This moss was the most common plant in the study area and occurred on 98-100% of plots measured. Average ground cover was about 60% (or a Braun-Blanquet average estimate of 5). On a seasonal basis the ground cover increased to a maximum of about 67% during winter and was reduced to a minimum of about 45% during spring and summer. During autumn the ground cover of Rhacomitrium was about midway between that of spring, summer, and winter values.

Hieracium pilosella had two separate months (April (24%) and August (22%)) of greater availability, but also showed a gradual increase over November and December leading to the greatest availability during December (28%). Hieracium was the second most common plant in the grassland occupying between 14 and 28% of the grassland and occurring on 95-98% of the plots. The minimum value of 14% was recorded during May and the maximum value of 28% during December. Hieracium was present in the largest amounts during summer and the least amounts during the latter part of autumn and first two months (June and July) of winter.

The grasses were most available during April (11%). Under the category of grasses in figs. 4.11 and 4.12 are grouped _Anthoxanthum odoratum_, _Holcus lanatus_ and _Agrostis tenuis_. This group showed a steady increase in ground cover over spring and summer and, surprisingly, into autumn (except May when grass decreased slightly). This increase was offset by a decrease during winter to a July to October minimum. The maximum of about 11% of total ground cover occurred during April. Grasses were least common during winter and spring. The most common of the three grasses was _Agrostis_ which made up between 2 and 7% of the total ground cover. _A. odoratum_ was the next most common grass and made up between 1 and 3%. _Holcus_ was the least common species and made up only 0.5 to 2% of the total ground cover.

The tussocks were most available during May (11%) and August (12%). The two dominant tussocks present on the study flat were _Poa colensoi_ and _Festuca novae-zelandiae_. Together these two species made up from 6 to 12% of the total ground cover. _Festuca_ was slightly more common than _Poa_ in terms of ground cover, but occurred on fewer plots than _Poa_. _Festuca_ occurred on about 15% of plots whereas _Poa_ occurred on about 28% of plots. Individual plants of the two species were of different sizes, _Festuca_ being the larger. The ground cover of the tussocks remained relatively constant throughout the year.

Those species grouped under 'others' showed the greatest monthly change during September (23%) when the availability of these species increased eight fold, indicating the presence of a large amount of spring growing/flowering species. This percentage cover increase was slightly reduced during October and much reduced, to about normal levels, during November with other smaller increases during December (12%), January (10%) and March (8%). There are 14 species grouped into this category. However, all species in this category typically occurred less and include plants such as the small ground hugging shrubs and seasonal species. As a group, the 14 species made up less than 5% of the total ground cover during autumn and winter. The dramatic increase in the ground cover of these plants during September was due to a relatively few species such as _Ranunuculus repens_, _Rumex acetosella_, _Luzula rufa_ and _Rytidosperma setifolia_, as the small shrubs such as _Pimelia prostrata_ and _Hebe pimelioides_ remained a relatively constant size thoughout the year. During summer some of the seasonal species began to die off (pers obs) resulting in a lessening of total ground cover in this grouping.

As could be expected from the relatively constant availability of the various plant types, no bare ground was noted on the study flat.

Statistical analysis of the results using Spearman rank correlations showed a largely negative correlation (r_s= -0.3060 to 0.0026,n=20) between the amounts available and the amounts eaten. When _R. lanuginosum_ was removed from the calculation (because of high availability but low consumption) the correlations between availability and consumption increased, so that during summer there was a high correlation (r_s=0.8059,n=16). Other seasons had moderate (autumn r_s= 0.3353,n=16) or low (winter r_s= 0.2412, spring r_s= 0.1735,n=16) correlations. When Rhacomitrium and juvenile hares also were removed from the calculations (because the lack of data for juveniles during spring when they are absent was overly influencing the analysis) the correlation increased once again, so that correlation was high during summer (r_s=0.7381,n=8), moderate during spring and autumn (r_s=0.3571 and r_s=0.4048,n=8 respectively) and low during winter (r_s=0.2619,n=8).

In summary (fig.4.12), Rhacomitrium was the most common plant in the grassland, making up between 45 and 67% of the total ground cover. Hieracium pilosella was the next most common plant occupying between 15 and 25% of the total ground cover. Grasses covered about 5 to 10% of the study flat and tussocks also about 5 to 10%. The sum of all other species varied between 2 and 15%, largely dependent on the season.

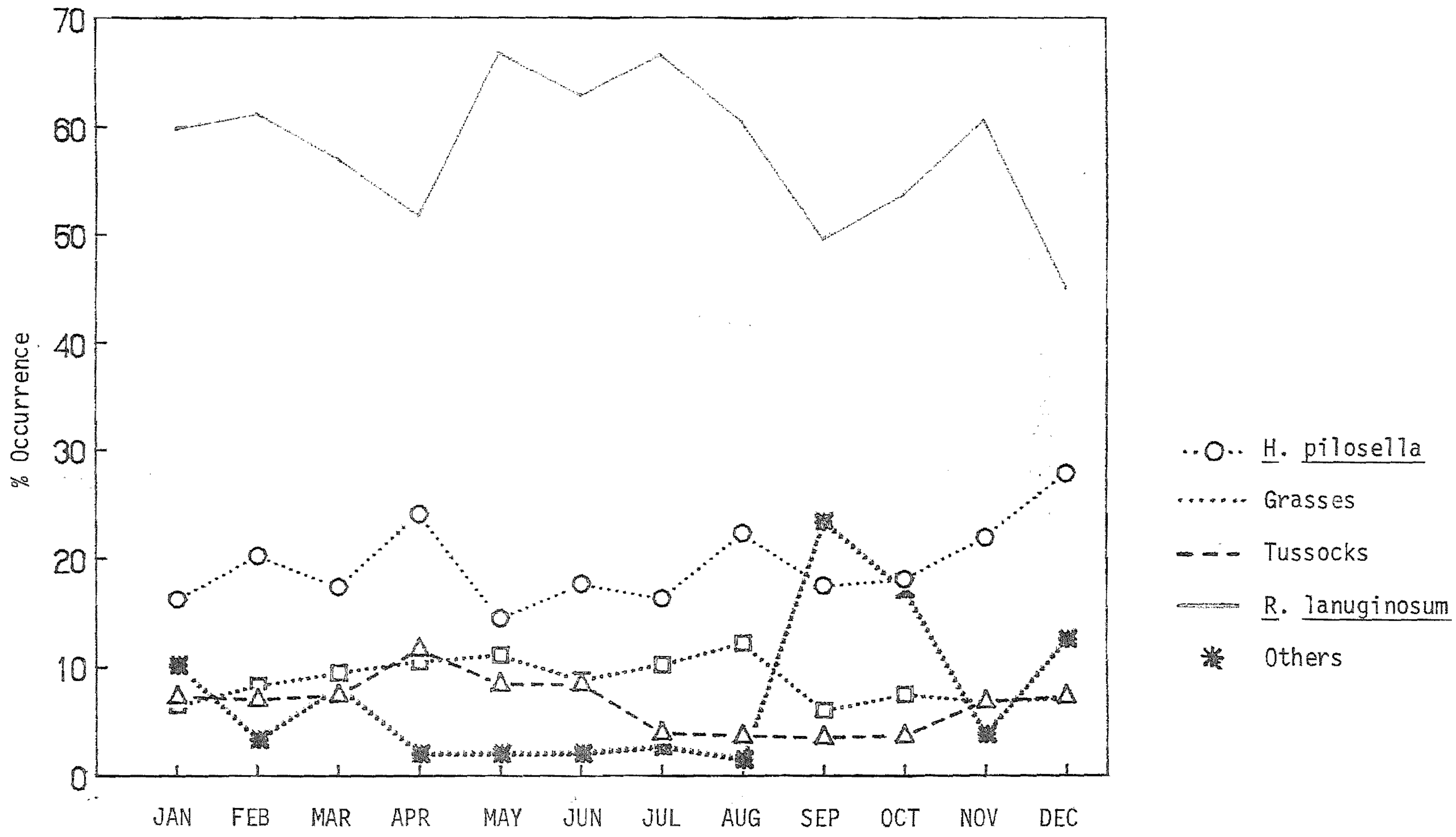


Figure 4.11: Monthly availability of plants in the study area.

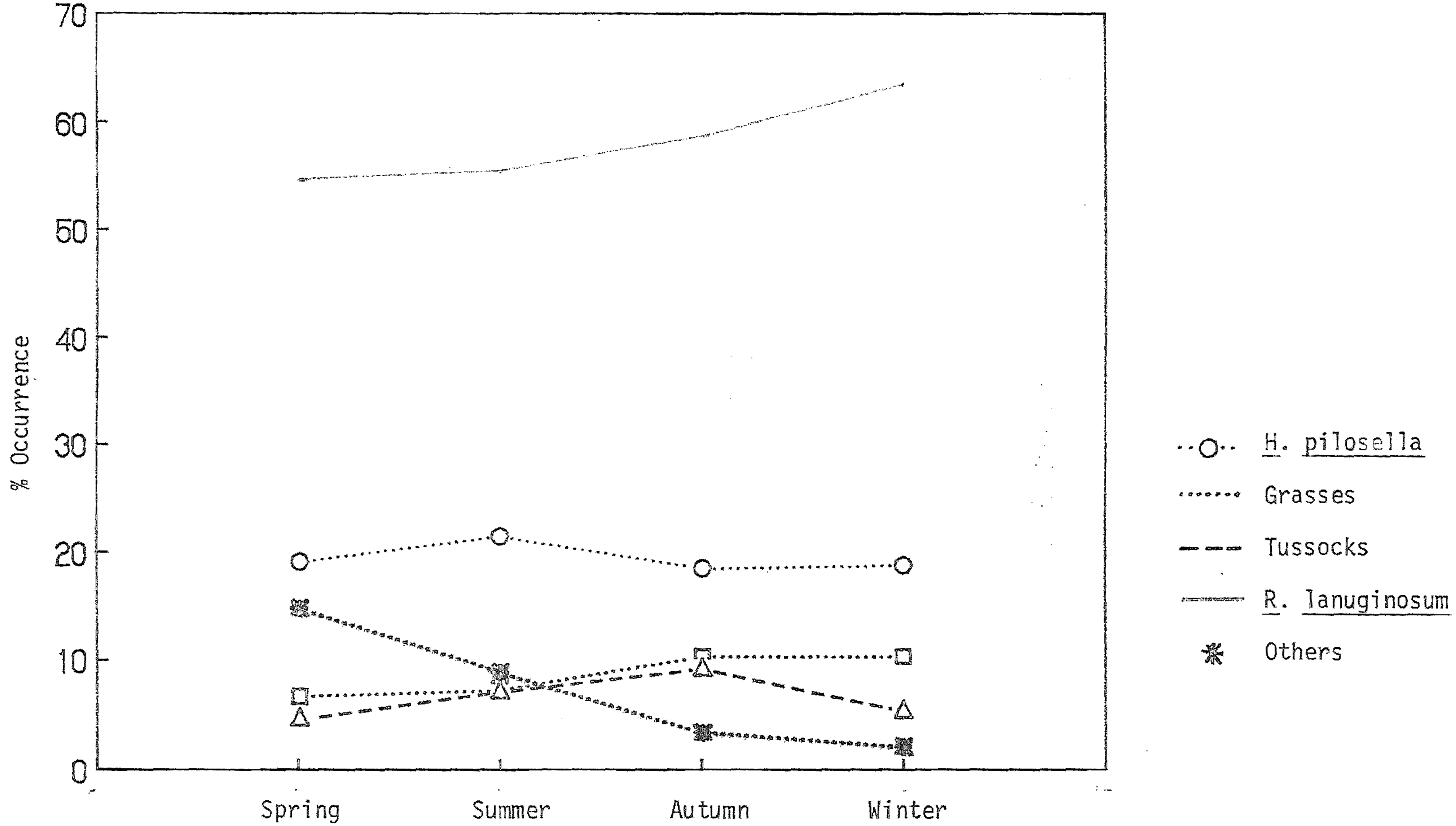


Figure 4.12: Seasonal availability of plants in the study area.

4.2.2 Exclosure Plots

Results for the exclosure and control plots are presented in table 4.2. These results should not be emphasised as they are an approximate estimate only due to the small number of samples. The plots measured during May (after six months or one growing season) gave an average weight of 107.07g for the six exclosure plots and 131.24g for the control or unfenced plots. This indicates that the control plots contained 18.5% more plant material than did the exclosure plots. Those plots measured during October (after 12 months or one growing season and one winter) gave an average weight of 81.21g for the exclosure plots and 101.29g for the control plots, or 19.9% more plant material on the control plots compared to the exclosure plots (table 4.2). Paired T-tests to determine whether the difference between means of exclosure and control plots were significant showed a significant difference in both May ($P<0.05$, $DF=5$, $n=6$) and October ($P<0.05$, $DF=5$, $n=6$).

The amount of vegetation per $900cm^2$ was 24.2% less after winter than it was before winter inside the exclosure plots and was 22.9% less on the control plots.

Table 4.2: Individual and averaged results from exclosure plots. Weights are in $g/900cm^2$.

Exclosure plot	wt	Control plot	wt
May			
1	84.41	1	145.76
2	110.07	2	131.20
3	104.07	3	119.06
4	65.54	4	98.47
5	134.28	5	156.13
6	144.08	6	136.78
Mean	107.07	Mean	131.24
October			
1	67.09	1	98.69
2	87.64	2	113.61
3	88.11	3	100.59
4	109.81	4	101.68
5	53.43	5	91.88
6	81.0	6	100.29
Mean	81.21	Mean	101.29

4.3 Calorimetry

Calorific analysis revealed no marked differences between the different food types in terms of maximum and minimum energy value (Table 4.3). Values tended to remain constant over the summer and autumn months (Fig 4.13) but then began to fluctuate over the winter months, becoming more stable again over the spring months.

Analysis of variance revealed that the difference between plant types was significant within a month ($F_{4,9}=6.42$, $P<0.01$) and also over the year (or between months) ($F_{9,36}=3.07$, $P<0.01$). However, even during spring the maximum difference between plant types was only 2.08 kcal/g (fig 4.13).

The minimum calorific value recorded was 4.11 kcal/g for Hieracium during May and Rhacomitrium during August and October, and the maximum value 6.19 kcal/g for Poa during September (Fig 4.13, Table 4.3). The range of values tended to decrease during winter (about 4.15 kcal/g to 4.96 kcal/g) with a minimum during July even though individual plant values were more variable. Maximum range of values occurred during spring (September 4.11 kcal/g to 6.19 kcal/g).

An index of the relative total calorific intake was calculated by multiplying the amount of a particular species eaten (as a percentage of the total diet) by the calorific value (in kcal/g) of that species. The results from this calculation showed an intake of energy throughout the year

Table 4.3: Maximum, minimum and average calorific value in kcal/g of major dietry items.

Species	Max	Min	Average
H pilosella	5.04	4.11	4.58
R. lanuginosum	4.64	4.11	4.28
P. colensoi	6.19	4.93	5.38
F. novae-zelandiae	5.60	4.18	4.98
Grasses	5.43	4.18	4.97

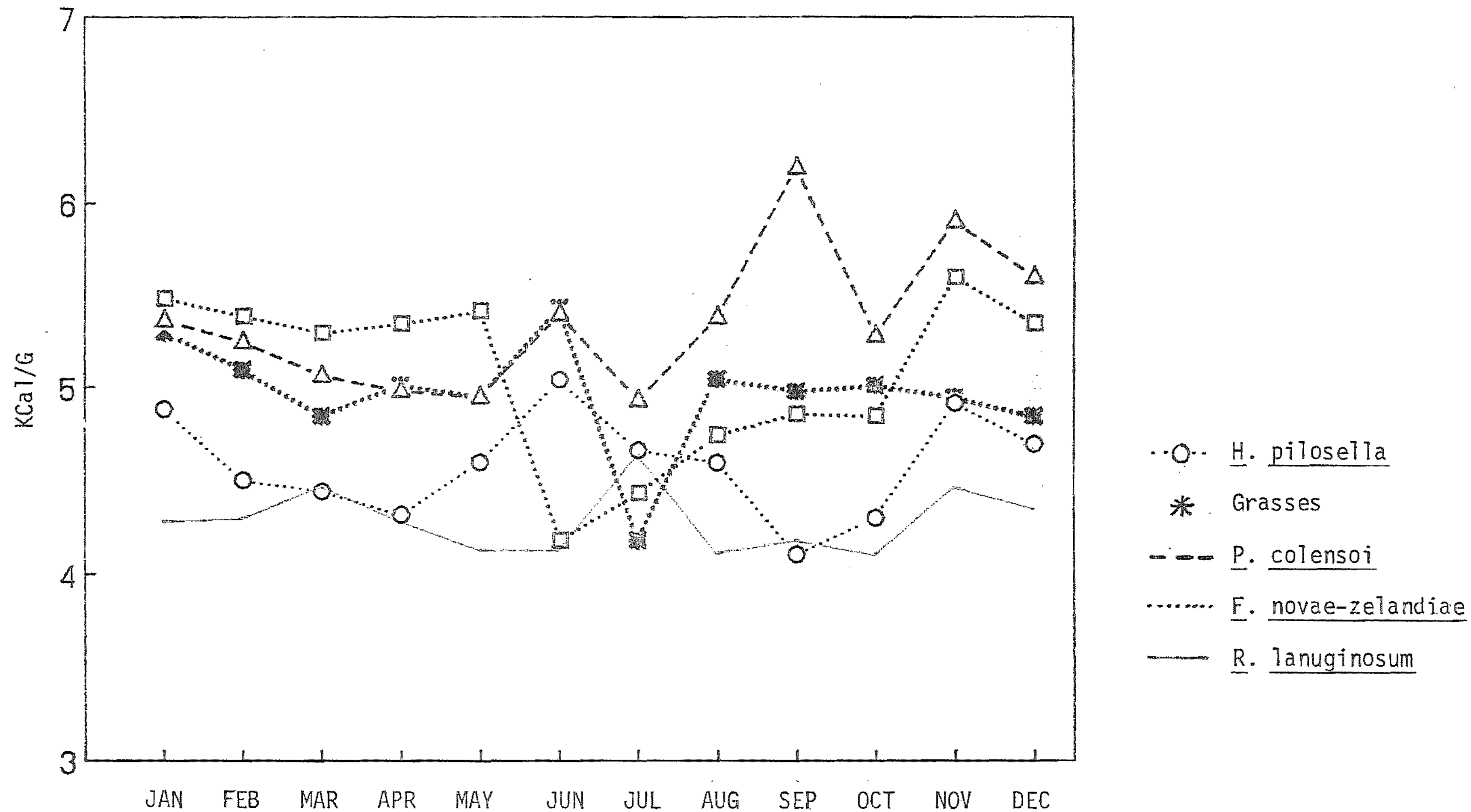


Figure 4.13: Monthly calorific values of major dietry items.

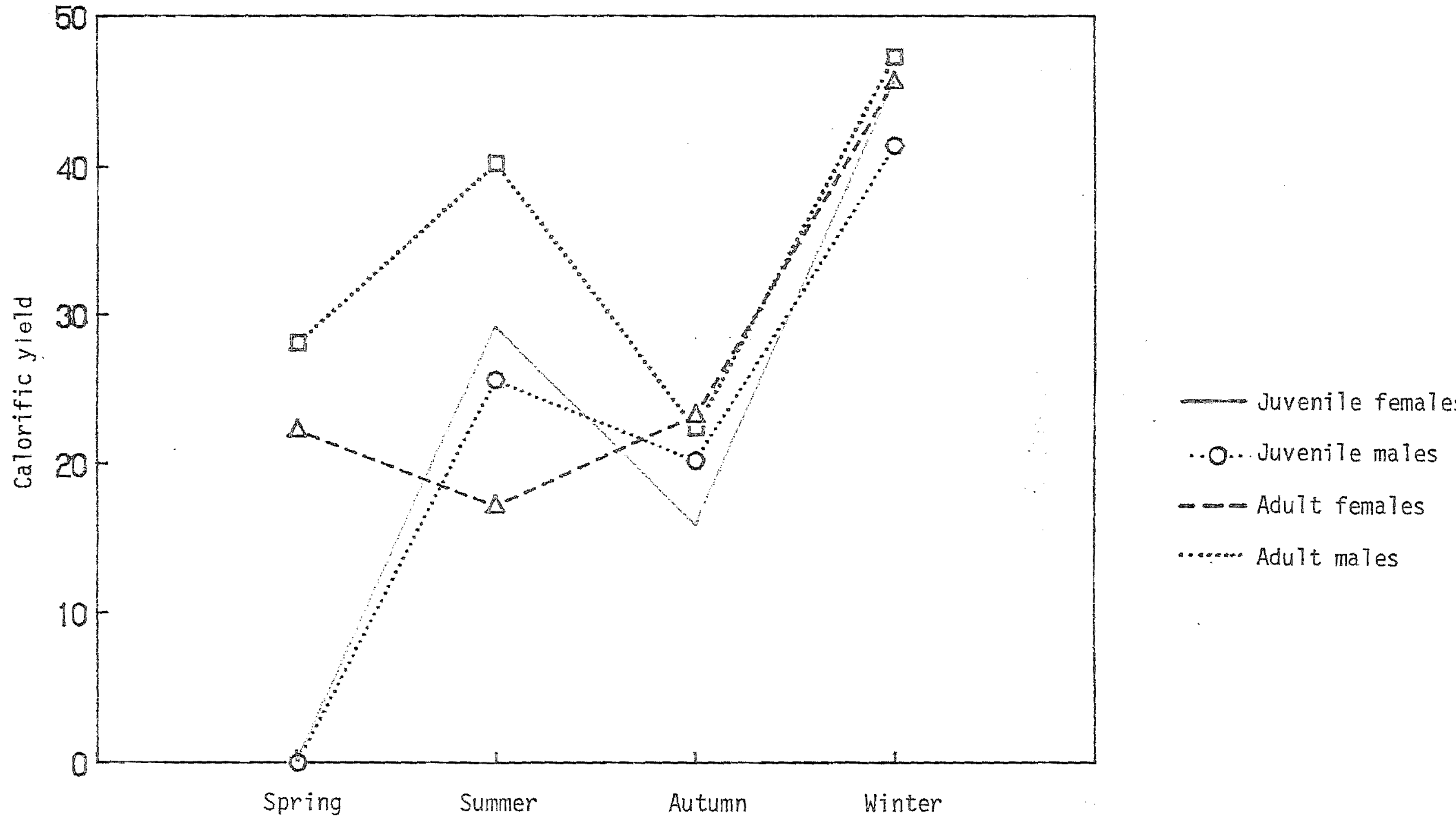


Figure 4.14a: Calorific value x amount eaten of *R. lanuginosum*.

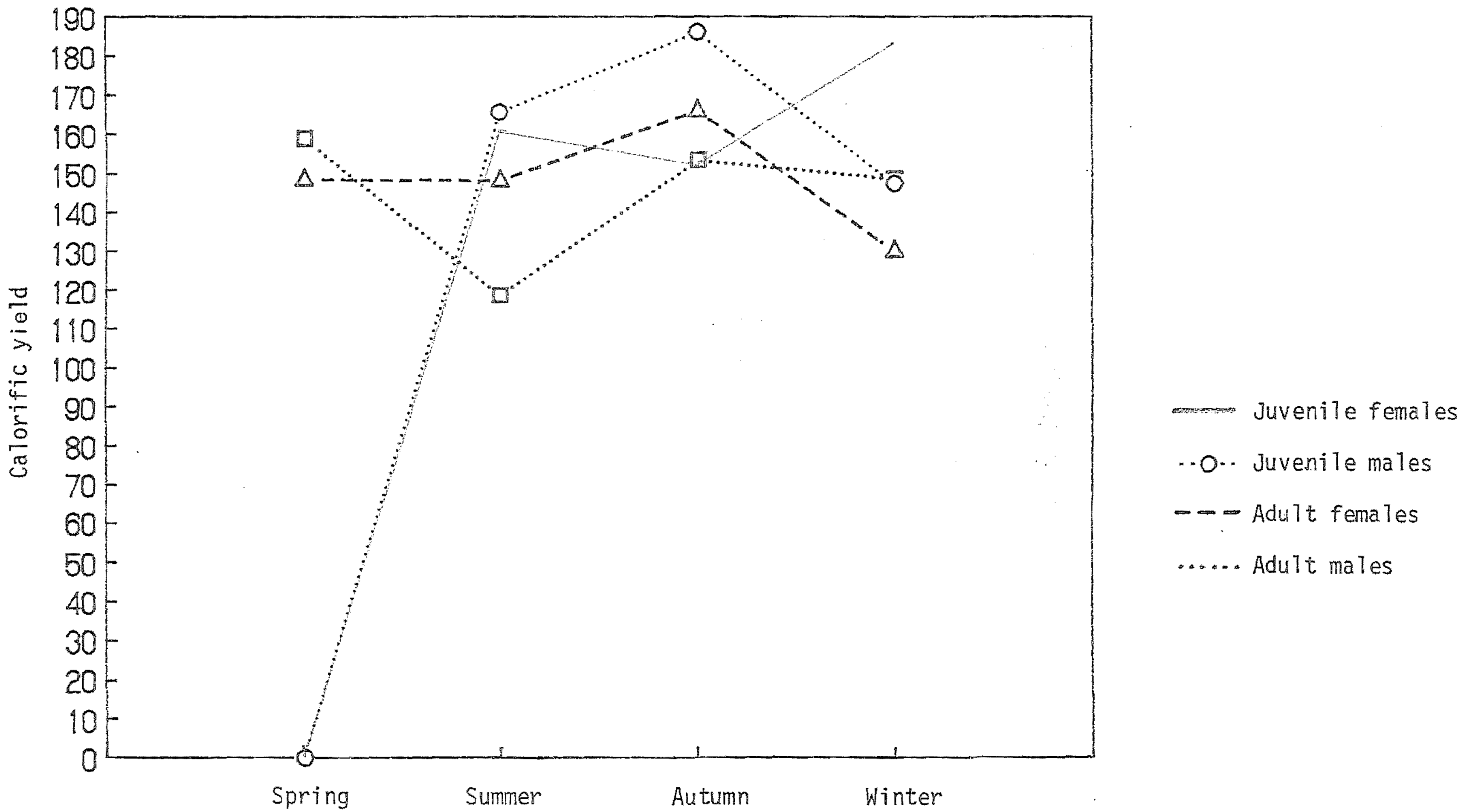


Figure 4.14b: Calorific value x amount eaten of H. pilosella.

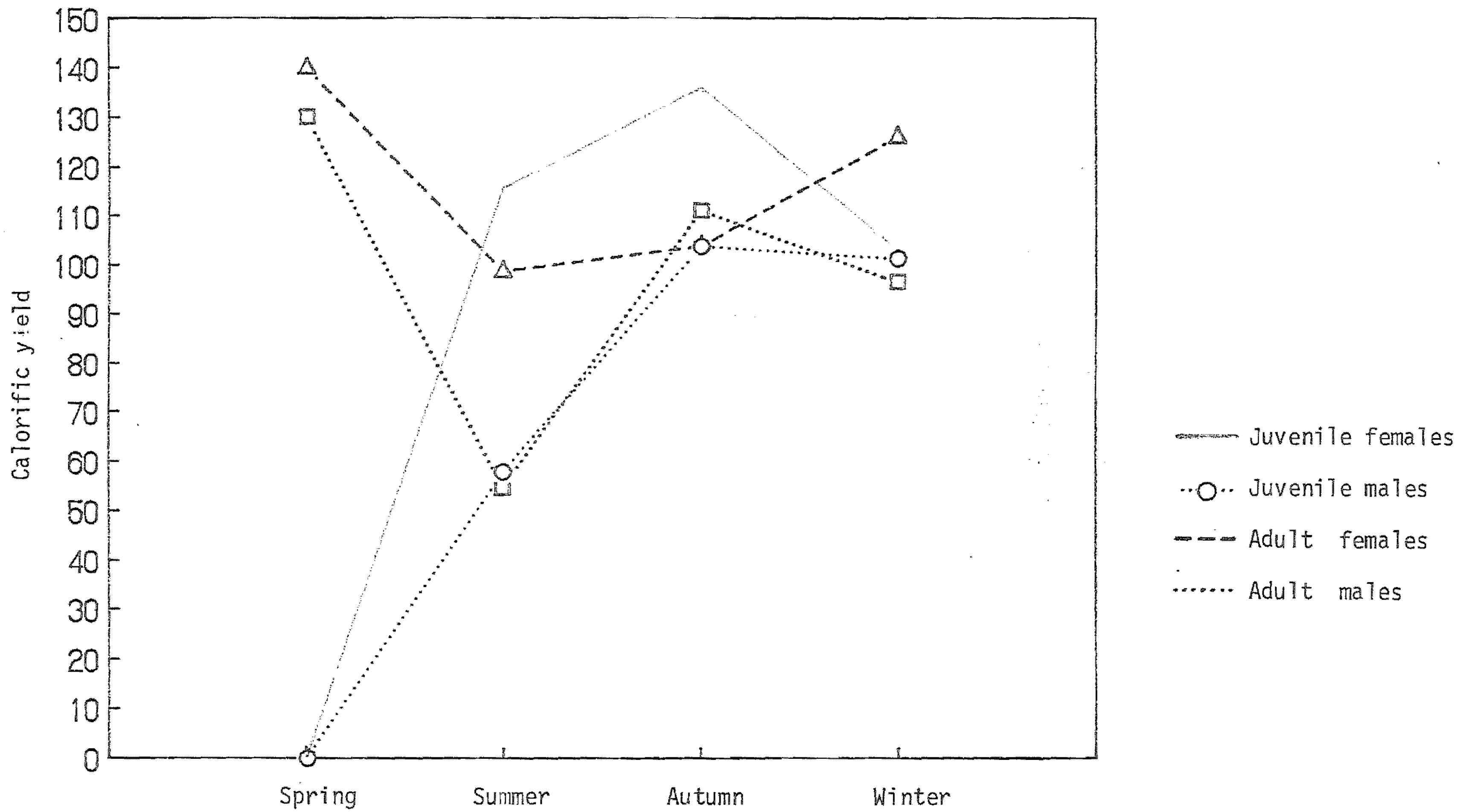


Figure 4.14c: Calorific value x amount eaten of the grasses.

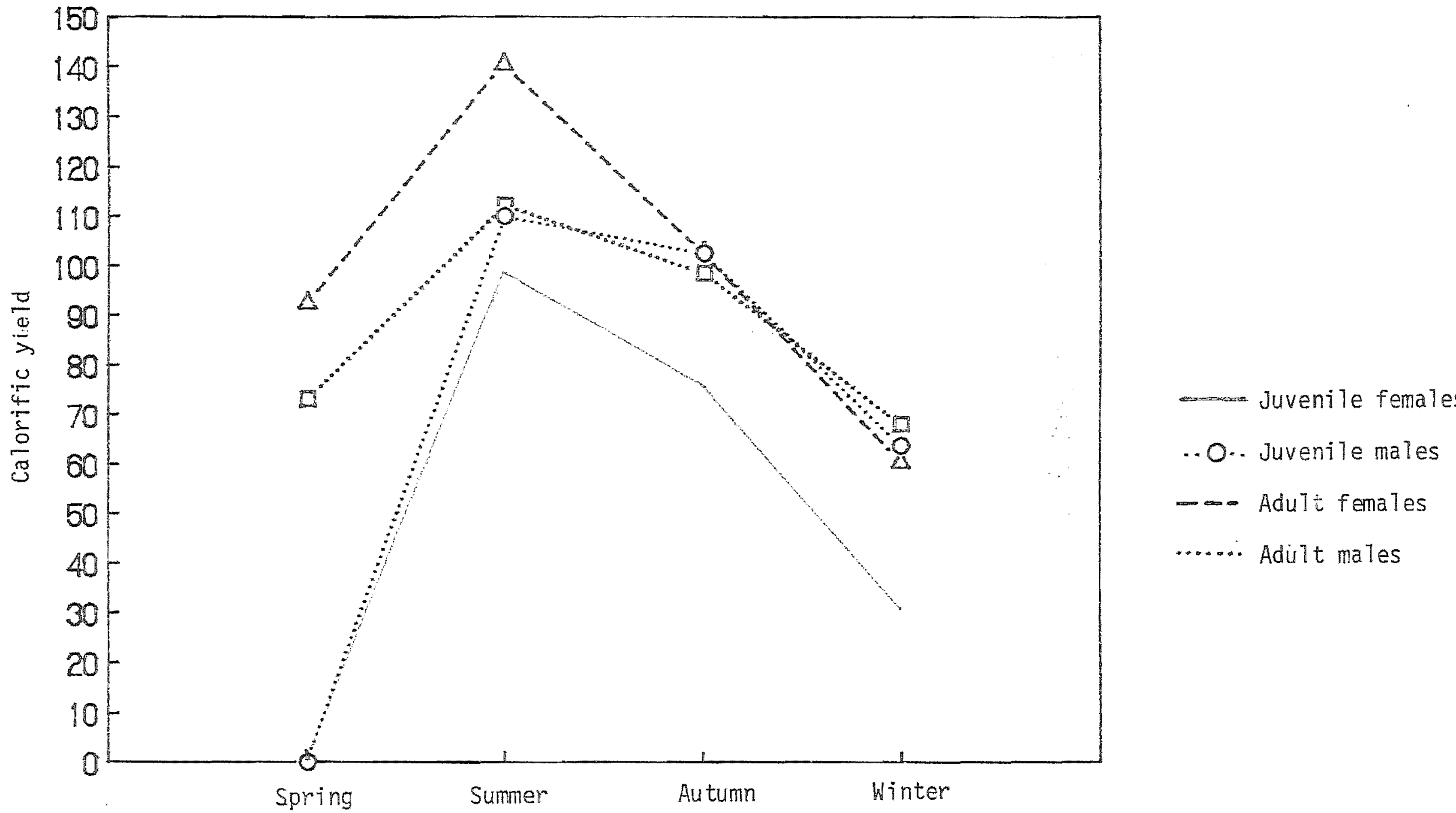


Figure 4.14d: Calorific value x amount eaten of the tussocks.

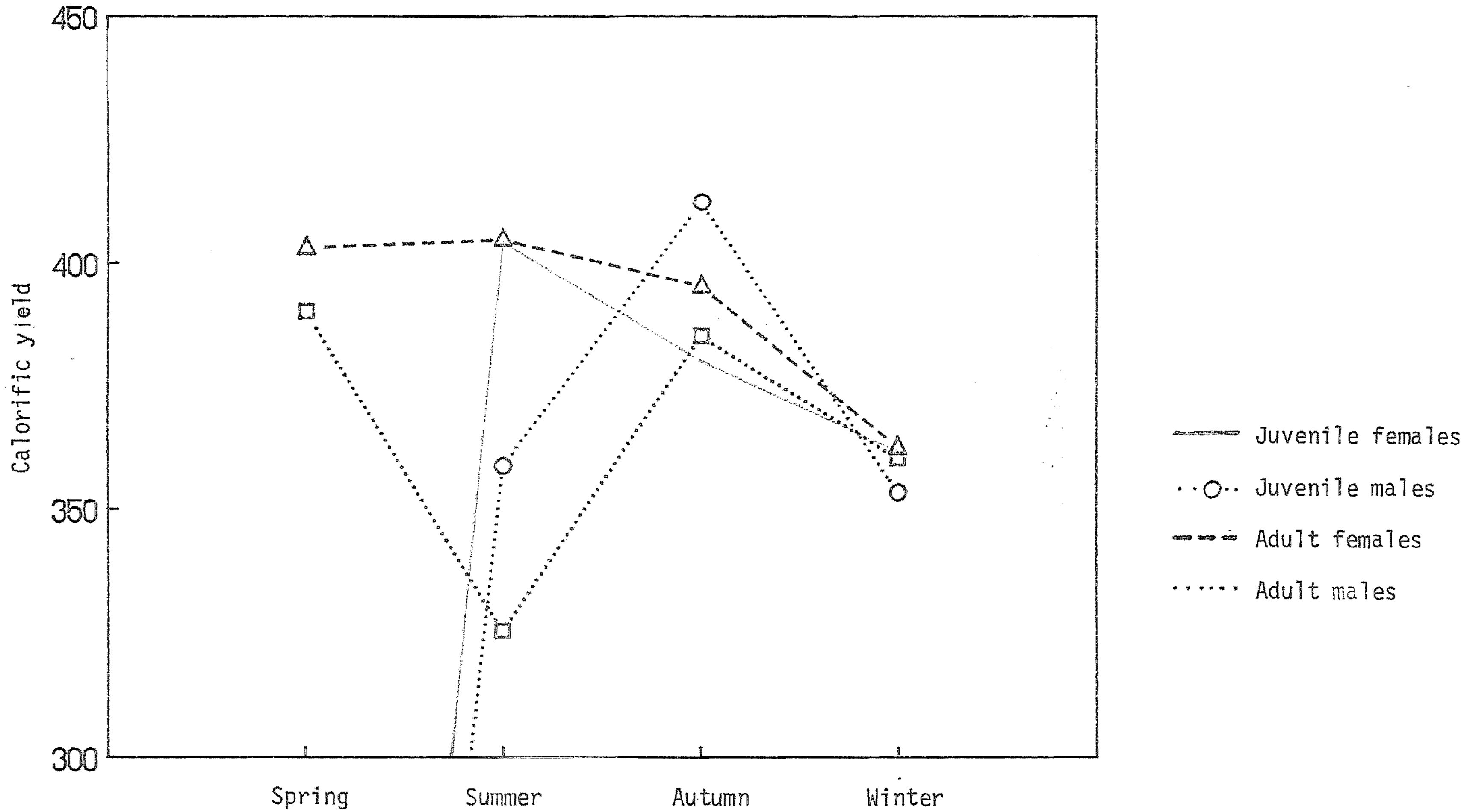


Figure 4.14e: Total calorific value of the major dietry species in all age and sex classes of hares. Sum of figures 4.14a- 4.14d.

which varied between 325 kcal/g and 404kcal/g (Fig 4.14e). When the calorific intake was divided into the four main plant types (Hieracium, Rhacomitrium, tussocks and grasses) it appeared that the energy gain from the different plant types varied so that as the energy yield from one decreased, the decrease was compensated for by an increase in consumption of another plant type. For example, as the energy yield from the tussocks decreased over the autumn winter period (Fig 4.14d) the yield from Rhacomitrium increased (Fig 4.14a).

4.4 Secondary metabolites

Three types of secondary metabolites analysis were undertaken on the food plants so that a more complete determination of any possible feeding deterents could be gained. Results from the Folin-Denis reaction ranked Hieracium pilosella as containing the greatest amounts of total phenols (78% absorbance). Three of the four other species analysed gave results within the same order of magnitude, but R. lanuginosum contained much lower levels of phenols (Table 4.4).

Monomeric tannins were measured by the Vanillin reaction (Ribereau-Gayon 1972). Results from this test are expressed as a vanillin value, V (see methods). It would appear from this analysis that F. novae-zelandiae contains the greatest amounts of monomeric tannins (V=16.5). Results from other species were much lower than this value with two species giving negative results, indicating very low levels of this type of tannin (table 4.4).

Condensed tannins were measured using the Leucoanthocyanin method (Ribereau-Gayon 1972). Compared with the results given by the vanillin reaction, the results for condensed tannins were somewhat surprising with Hieracium containing much higher levels of condensed tannins, whereas the grasses contained none and Rhacomitrium very little. Of the two tussocks Festuca contained the greatest amounts of condensed tannins, with Poa containing less than half the amount in

Festuca (Table 4.4).

Rankings are summarised in table 4.5. In drawing up this table all three tests were given equal weightings. If the two, tannin results are combined and given equal weighting with the phenols results (table 4.6), _Festuca_ and _Hieracium_ are distinguished as fourth and fifth rank respectively, while the other three species retain the same rankings. However, condensed tannins, in particular, have been shown to have a great effect in the choice of food plants by monkeys and apes (Bate-Smith 1972 (from Harbourne 1988)). Therefore it is probably more valid that all three categories should have equal emphasis.

Table 4.4: Secondary metabolite content of major dietary items. Phenols and condensed tannins are expressed as percent absorbance and monomeric tannins as a V value (see methods for a more detailed explanation).

Species	Phenols	Tannins Monomeric	Tannins Condensed
R. lanuginosum	47	-14.0	1
P. colensoi	63	3.9	7
Grasses	71	6.9	0
H. pilosella	78	-10.6	62
Festuca novae-zelandiae	68	16.5	19

Table 4.5: Ranking of major dietary items in relation to content of secondary metabolites (1=least, 5=most) and overall rank.

Species	Phenols	Tannins Monomeric	Tannins Condensed	Overall Rank
R. lanuginosum	1	1	2	1
P. colensoi	2	3	3	2
Grasses	3	4	1	3
H. pilosella	4	2	5	4
F. novae-zelandiae	5	5	4	5

Table 4.6: Ranking of major dietary items when monomeric and condensed tannins are combined and given equal weighting with phenols. The rankings of the individual tannins have been combined and averaged, and the result combined with the rankings of phenols to give an overall ranking with tannins and phenols having equal weightings.

Species	Phenols	Tannins	Av.Tannins	Total	Rank
R. lanuginosum	1	3	1.5	2.5	1
P. colensoi	2	6	3.0	5.0	2
Grasses	4	5	2.5	6.5	3
F. novae-zelandiae	3	9	4.5	7.5	4
H. pilosella	5	7	3.5	8.5	5

4.5 Neutral detergent fibre analysis

The results gained from the neutral detergent fibre (NDF) analyses are summarised in table 4.7 and Fig 4.15. Four of the five plant types measured appeared to give relatively constant values for all the seasons, but analysis of variance indicated that there was a significant difference between seasons ($F_{3,12}=5.95$, $P<0.01$) for each species. Poa colensoi was the only species to vary by more than 10%, all the others having a maximum range of about 8%. Analysis of variance also showed a significant difference in NDF content between species ($F_{4,3}=28.71$, $P<0.01$).

The most digestible species was H. pilosella (fig 4.15) which varied between 23% NDF and 30% NDF. The other four plant groups (R. lanuginosum, P. colensoi, F. novae-zelandiae and the grasses) all had a higher NDF content, the minimum percentage (58%) for these four being almost double the maximum value for Hieracium.

The species with the highest average NDF contents were Festuca (73.25%) and Rhacomitrium (71.95%) (Table 4.7). Poa (66.47%) and the grasses (61.57%) had the next highest fibre content compared with Hieracium with an average value of 26.61%.

In summary, Hieracium was found to be much more digestible than the other species measured. The other four plant types measured had NDF contents within the same range as each other and had fibre contents greatly in excess of Hieracium.

Table 4.7: Seasonal and average percent NDF values and ranking for major dietary items for all seasons (1=lowest).

Species	Spring	Summer	Autumn	Winter	Average	Rank
H. pilosella	29.47	27.02	26.62	23.36	26.61	1
Grasses	59.70	63.66	64.97	58.17	61.62	2
P. colensoi	70.08	73.66	64.05	58.34	66.53	3
R. lanuginosum	72.38	66.15	76.42	73.02	71.99	4
F. novae-zelandiae	77.08	71.56	71.92	72.65	73.30	5

Table 4.8: Calorific value x amount eaten (as a percentage of the diet) x inverse of the NDF value. Shows approximate total calorific yeild from the major components of the diet for each season.

Age/sex class	Spring	Summer	Autumn	Winter
Juvenile female	0	201.2	192.0	196.1
Juvenile male	0	185.0	213.7	178.3
Adult female	197.6	195.0	199.8	175.5
Adult male	197.0	153.8	192.1	180.3

Table 4.9: Calorific value x inverse of the NDF content. Shows approximate calorific yeild from the individual major dietary components for each season.

Species	Spring	Summer	Autumn	Winter
Hieracium pilosella	3.26	3.41	3.26	3.50
Rhacomitrium lanuginosum	1.19	1.21	1.20	1.20
Poa colensoi	1.93	1.81	1.67	1.75
Festuca novae-zelandiae	1.87	1.98	1.96	1.63
Grasses	1.91	1.95	1.89	1.87

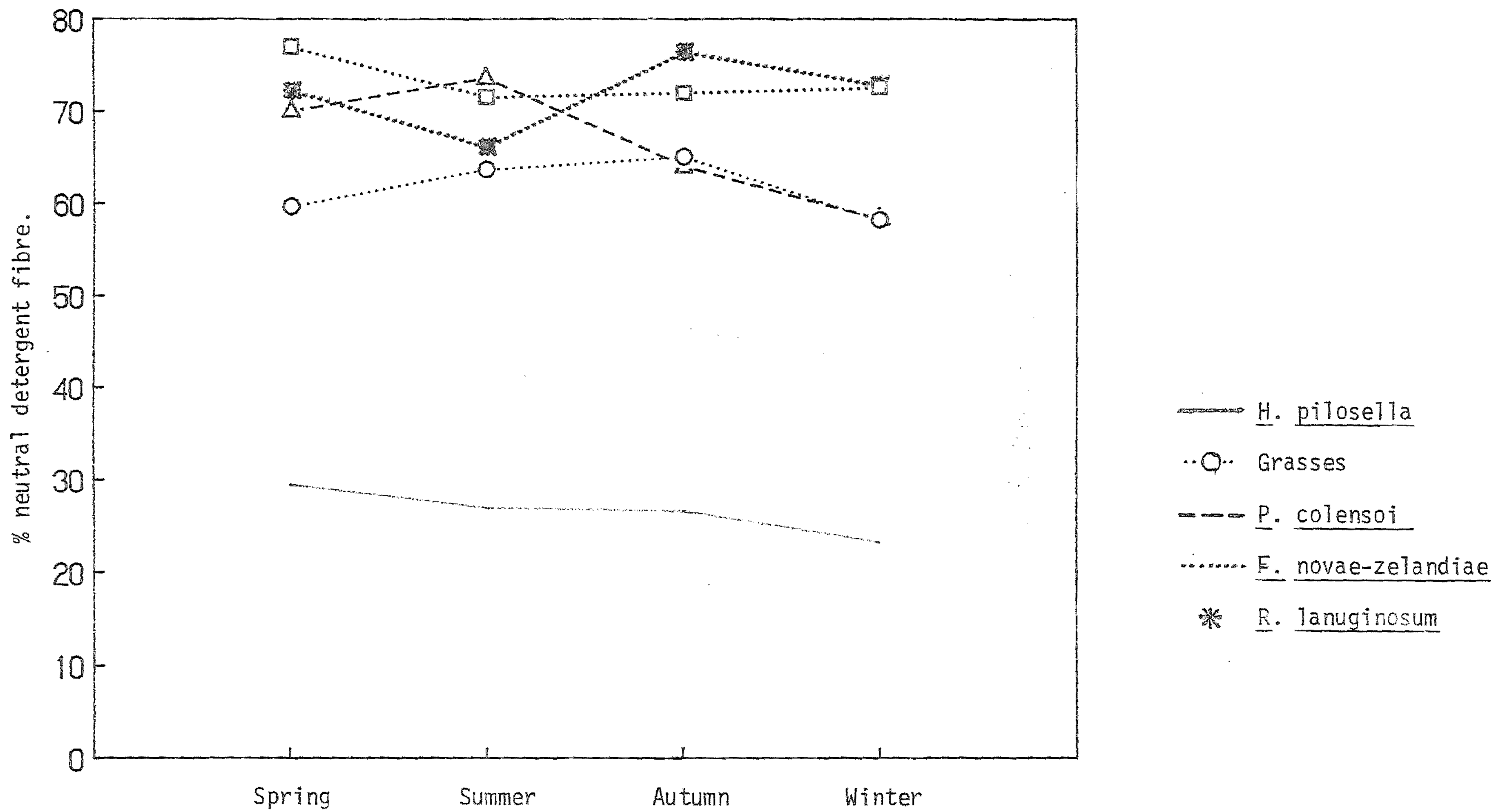


Figure 4.15: NDF content of major dietry items.

Further to the index of calorific value x the quantity eaten another index was created by multiplication of the inverse of the percent NDF content. The average %NDF of a species was expressed as a proportion of one and subtracted from one so that the inverse was obtained. This figure was then multiplied by the result from the calorific value x quantity eaten equation to give an approximate calorific yield in proportion to the amount eaten of each species and also of the total calorific intake from a given intake of food plants. The result from this multiplication revealed a more constant intake of calories for all age and sex classes over the year, with values varying by only 59.9 calories (Table 4.8). Within a season the figures were mostly within 25 calories of each other, the only exception to this being during summer where adult males had a lower intake than any of the other categories.

An index of calorific value x inverse of the NDF content was also created to give an approximate figure for the amount of energy that was actually available from each plant species for each season (Table 4.9). Hieracium showed the greatest yield of calories per gram with all other species being much the same. Rhacomitrium was on average the species with the lowest yield of calories per gram.

Chapter 5 : Discussion

The hares diet can be divided into five main categories of plants ie. *Hieracium pilosella*, grasses, tussocks, *Rhacomitrium lanuginosum* and other minor species. Of these the major constituents of the diet were *H. pilosella*, grasses and the tussocks. These three plant types constituted up to 94% of the total diet at any one time. Results of the gut sample analysis revealed that the hares in this region are relying heavily on *Hieracium pilosella* as their major food item. Reliance on one or two species has also been shown by several other authors for various mammals, with up to 90% of the diet being of one species for hares (Horne 1978; Parker 1977; Giuletti and Jackson 1988; Hewson 1962), jackrabbits (Flinders and Hansen 1972), possums (Coleman et al 1985), and goats (Mitchell et al 1987). Several reasons have been put forward to explain this, but the general consensus appears to be that the major dietary item is in fact the dominant plant in the study area. The constant relatively high intake of *Hieracium* found in the present study follows this general rule.

The grasses also make up a major portion of the diet (10.2-27%) and are a common group of plants in the area. The three species of grass have been combined in the analysis because it is unlikely that hares would be capable of making a clear distinction between the different species when feeding. There is a slight difference in the relative consumption of the various grass species by juveniles and adults. Agrostis tenuis is the most commonly eaten grass by juveniles with Anthoxanthum odoratum being more favoured by adults. This difference may be due to some metabolic or physiological reason, but there are no data to confirm this suggestion.

The constant high consumption of Hieracium and the grasses indicate a relatively constant diet of the hare population as a whole throughout the year. However, statistical analysis indicates a highly variable diet for the different age and sex classes with adults and juveniles, and males and females, all differing in their diets as well as each having diets that vary throughout the year. The difference between adult and juvenile diets could be explained in terms of different metabolic requirements, as could the difference in male and female diets. Hewson (1977) found in L. timidus that during the period when female hares were pregnant and/or lactating they chose a diet containing more nutrients (N & P) than did males during the same period, indicating that physiological requirements may indeed be a determining factor in diet selection at various times of the year. Miller (1966) found a similar selection. Seasonal variation in diet has also been shown by other authors (Flux 1962, 1967(b); Hewson 1962; Currie and Goodwin 1966; Flinders and Hansen 1972).

The relatively low occurrence of the moss Rhacomitrium lanuginosum in the diet was at first somewhat surprising. However, the consumption of Rhacomitrium increased quite dramatically during winter, perhaps indicating that while it is not a preferred food item, it will be eaten if there is a short supply of other foods. Other researchers have shown that the consumption of non-preferred species will increase if preferred food items are not available or in short supply (Flux 1967(b); Andelt et al 1987; MacArthur and Pianka 1966). The increase in consumption of Rhacomitrium appears to be accompanied by a reduction in consumption of the grasses during a season when these plants are less available and perhaps less preferred. A marked increase in consumption is also apparent in the consumption of the Carmichaelia species. During summer these two plants were rarely eaten, but during winter comprised up to 12.2% of the total diet. Switching such as this could be due to one of two factors ie. an increase in desirability due to increased nutritional value, or a lower availability of preferred species, or a combination of both factors. Sinclair et al (1982) have shown that snowshoe hares maintain a relatively constant intake rate as the quality of food falls, further reinforcing the hypothesis of MacArthur and Pianka (1966), that diet expands to include more species when food is scarce and contracts to preferred species when food is abundant. This study has also indicated that an increase in the variability of the diet occurs when preferred food plants are more scarce. However, it must also be taken into account that appetite, previous feed experience and the extent, type and spatial distribution of forage available can, and most likely will, have an effect on the diet (Hercus 1960; Emlin 1966).

Consumption of species listed under 'others' remains reasonably constant throughout the year. These species can be thought of as 'fillers' in the hares' diet and are species that are eaten in low and variable quantities, and that are perhaps eaten by the hares either to increase the variability of their diet (Hughes 1979), or tried as potential food items and perhaps rejected after a small quantity has been eaten. Most of the plants in this category are available in relatively constant amounts throughout the year (except September and October), so any increase in their occurrence in the diet is not due to an increased availability.

From the data obtained during the monthly vegetation survey it became apparent that there was little change in the seasonal occurrence of the various plant species. Most species in the grassland remained at fairly constant levels and it appears that the main variation was due to an increase in a few seasonal species during spring, and to a lesser extent summer. The increase in the species listed under others occurred principally during September, with values for October, December, January and March also being higher than average (see fig. 4.11). The extent and occurrence of Rhacomitrium appears to be largely determined by the availability of moisture. Rainfall is higher during winter in this area (NZ Met. Service) and consequently the moss swells and grows (pers obs). However, during the drier summer months this moss is reduced to a dry, brittle remnant. Therefore it appears that this species is limited by the amount of water available rather than the temperature.

Hieracium pilosella also showed a slight seasonal variation in ground cover. The variation was due to this species expanding during the warmer spring and summer months by increasing individual leaf area and also by producing more leaves per plant (pers obs). The growth form of Hieracium also became more erect during the warmer months, thereby making the plant more available as a food item for the hares.

Although the tussocks made up only 5-10% of the total ground cover and were scattered throughout the grassland their erect growth form made their availability to herbivores much greater than would be expected from these results. For example, although a tussock may occupy a ground surface area of 5% of an individual plot, the same tussock may stand 20-30cm high, so that in effect the amount available to herbivores is much greater. Therefore when comparing the availability of any species as a food item for hares frequency of occurrence, ground cover and an estimate of biomass and ease of cropping should be taken into account.

The grasses were most common during autumn. This is probably due almost entirely to the availability of water once again (pers obs). During spring there was probably a sufficient amount of precipitation, but temperatures were still relatively cool. Summer in this area tends to be very dry (pers obs) and the study flat soil contained very little moisture. However, during autumn rainfall increased and temperatures were still sufficiently warm to allow some growth. The grasses, which had been slowly growing throughout spring and summer, suddenly showed some dramatic growth just prior to the onset of winter. The production of seedheads during the earlier summer months may also have been a sufficient draw on resources to prevent vegetative growth until early autumn.

Hieracium pilosella is becoming a major problem in high country South island areas. It is a relatively recent importation and occurred in very low abundance in the Avoca region as little as 25 years ago (Rose 1983). However this species increases in abundance in a logistic fashion and consequently has virtually taken over all the low altitude grasslands in this area (Rose 1983). Rose has found evidence of a general succession away from short tussock grassland in this area over the last 25 years, with two distinct phases. The first transition is to open Anthoxanthum odoratum/short tussock swards and the second phase is from the open A. odoratum/short tussock sward to a moderately closed Hieracium spp/exotic grass sward. The study flat appeared to be at a point midway between these two phases, with Hieracium in relatively high abundance but with the short tussocks also reasonably common. Exotic grasses also appeared to be on the increase (pers obs). According to Rose (1983) the end point of this succession is a reduction in bare ground and the amount of native grasses. No bare ground was encountered during this vegetation survey. There may have been a number of reasons responsible for the succession occurring but Rose considers the influence of man (through fires and the introduction of exotic flora and fauna) as the main factors.

Diet selection

The availability of the various food items selected by the hares on the study site remained relatively constant throughout the year. Diet was shown to vary throughout the year, but correlations between the amounts available and the amounts eaten also showed moderate to high probabilities during some seasons. Therefore it would appear that the hares are eating mainly what is available but are also making some choice of which plants to consume, because of the relatively constant availability of the favoured food items such as *Hieracium pilosella* and the grass and tussock species. Flux (1962, 1967(b)) found in Cupola basin that the hares diet varied between summer and winter. *Chionochloa* spp. and *Celmisia* spp. were favoured during winter and *Poa colensoi* during summer. However, Flux (1967(b)) notes that during winter *Chionochloa* spp. and *Celmisia* spp. were both available on ridges cleared of snow by the wind, whereas most of the *Poa* was covered by snow. The marked increase in *Poa* consumption coincided with snow melt. Horne (1978) found that the plants eaten by hares in Tongariro National Park reflected the plants general availability. Other authors whose findings show that the major food item was the main plant in the habitat include Hewson (1962), Miller (1966), Flinders and Hansen (1972), Parker (1977), Flinders and Crawford (1977) and Giuletti and Jackson (1988). However, there does appear to be evidence for some selection even amo ng these studies. For example, Horne (1978) found that an approximately 15% increase in _Festuca_ consumption during December coincided with a decrease in moss consumption during the same period, indicating a switch to the new seasons growth of _Festuca_. This study found that the major plants in the study site (except _Rhacomitrium_) make up the major portion of the diet, indicating little preferential selection. However, among the least available plants there appears to be some more definite preferences. The _Carmichaelia_ spp. are consumed in relatively large quantities during winter (PFO=7-15%) but consumption decreases markedly during summer (PFO=1-7%). No basis was found for this change. Sinclair et al (1982) found that hares maintained a relatively constant energy intake rate as food quality and quantity fell and therefore increased intake of lower quality food items and this could be occurring with the hares in this case. _Carex coriacia_ and _Rumex acetosella_ also show a definite seasonal difference in consumption, but summer is the season of highest consumption of these species, which would seem to conflict with MacArthur and Pianka's (1966) hypothesis.

The results from the exclosure plots suggest that the vegetation on the study flat is benefitting by having some grazing pressure or that the exclosure plots themselves altered some other factor in an adverse way. It is unlikely that the exclosure plots themselves would have altered any environmental conditions to an extent that would effect plant growth, because they contained no structures that could have affected wind, water, nutrient or light penetration. That vegetation benefits by having some grazing pressure has been suggested by Owen (1980) and Stenseth (1978). Owen (1980) has supported his argument with examples and Stenseth (1978) has backed these examples with mathematical models which show that Owen's hypotheses are possible. Perhaps the most valid example that Owen gives is that of the grasses, which survive best when cropped and are, as he states, probably totally co-evolved with grazers. However, evidence to support these hypotheses is largely circumstantial and requires further research. Herrera (1982) states that the hypothesis of Owen and Weigert (1981) that grasses and grazers represent a highly co-evolved system which has evolved on the basis of a mutualistic relationship lacks concrete evidence and is unlikely. Another possible explanation for there being more growth on the control plots is that animals still had access to, and therefore could defecate and deposit nutrients on the control plots, whereas the exclosure plots had no similar means of increasing the nutrient content of the soil. Transfer of nutrients has been supported by Owen (1980) as another benefit from grazing by herbivores.

The limited number of plots examined on such a diverse and patchy grassland as the study site can at best give only an indication of what is happening and I consider that the results cannot be extrapolated further.

The narrow range of calorific values for the food species was not entirely unexpected because researchers at Lincoln College working on pasture species have found little variation in values for most species (D. Poppi pers comm.). However, the sudden and relatively dramatic variations occurring during winter were unexpected. A possible explanation for these variations could be that the onset of winter, and the subsequent frosts and cold weather, causes the senesence of some plant tissues, and retraction and/or relocation of some plant metabolites to other areas of the plant. An increase in dead plant material was noted at this time of the year, as was a general shrinking of most plants on the study site.

The calorific values alone cannot be used to any great degree to explain the choice of food plants by the hares, because other features of the food plant may prevent the hare from taking full advantage of the calories potentially available. For example, a plant, such as a tussock, may have a relatively high calorific value, but an excessively high fibre content may prevent efficient digestion and use of the potentially available calories.

Other studies have also found no correlation between calorific content and intake of food items for hares (eg. Bryant 1979; Pehrson 1979). Miller (1966) found that hares preferred to feed on fertilised rather than unfertilised areas, but showed that the choice was due to higher levels of N and P. However, Horne (1978) found no relationship between plant choice by hares and the chemical composition of those plants.

Although the results from the secondary metabolite analyses gave only gross relative figures, with no specific details on the phenols or tannins present, they nevertheless provided further useful information about the possible reasons for plant choice by the hares. It would appear that tannin content is much more variable between these plant species than phenol content. The results from the Folin-Denis reaction (except Rhacomitrium) vary by only 15 percentage points, a very small amount with such a non-specific test. Rhacomitrium contains much lower amounts of phenols than the other plant species. These relatively constant results contrast with the results obtained from the tannin analyses. Monomeric tannins were more consistent between plant species than condensed tannins, but the difference was still relatively large with a spread of V=27.1. Condensed tannins were much more variable than either phenols or monomeric tannins with a maximum difference between species of 62% absorbance. Grasses contained no measurable amount of condensed tannins and Rhacomitrium contained very low amounts of condensed tannins. The most surprising result was that for Hieracium which recorded a relatively very high content of condensed tannins in contrast to its very low content of monomeric tannins. A possible explanation for this result is that the leaves of Hieracium had been retained for more than one year and were therefore of a greater age and consequently contained more condensed tannins due to this accumulation. The same reasoning could be applied in reverse to the very low reading for grasses, because all the leaves analysed were the newer green shoots of the current seasons growth. The lowest reading was once again for Rhacomitrium.

If all three measurements of secondary metabolites are taken into account and given equal weighting it would appear that a general ranking of plants from lowest to highest content of secondary metabolites would be as follows:

1. _R. lanuginosum_
2. _P. colensoi_
3. Grasses
4.= _H. pilosella_ & _F. novae-zelandiae_

Hieracium and _Festuca_ have the same cumulative rank (see table 4.2). However, _Festuca_ contained relatively large amounts of all three compounds, whereas _Hieracium_ contained the greatest amounts of two (phenols and condensed tannins) but very low amounts of the third (monomeric tannins). Because _Festuca_ had a consistent content of all secondary metabolites measured and _Hieracium_ varied by such a large amount, I would rank _Hieracium_ fourth and _Festuca_ fifth in the overall impact of the three secondary metabolites analysed.

Secondary metabolites did not appear to affect plant choice. Condensed tannins have been shown to affect the choice of many herbivores, including apes and monkeys (Bate-Smith 1972 (from Harbourne 1988)). In this study monomeric tannins were most closely correlated with actual plant choice, with _Hieracium_ having the lowest value (V=-10.6) of the vascular plants while also having the highest consumption. However, in contrast _Hieracium_ had the highest content of both phenols and condensed tannins and therefore in this study phenol or condensed tannin content did not seem to show any correlation with plant choice. Therefore there is some indication that the consumption of plant species may be related to the content of monomeric tannins but not to the other secondary metabolites measured. Results from the phenol and condensed tannin analyses both gave results indicating high levels of both of these secondary metabolites in Hieracium. These results conflict with the results of the gut sample analysis, which show Hieracium to be the major food item, because high phenol and condensed tannin content would be expected to act as a deterrent.

Plant toxins often act as digestion inhibitors (Bryant 1981) or feeding repellents through a warning signal of a visual or olfactory nature (Harbourne 1988), or cause a general decrease in metabolic rate (Thomas et al 1988). Wild herbivores have been shown to be well adapted to plant secondary metabolites and in many cases have evolved detoxification mechanisms (Freeland and Janzen 1974; Lindroth and Batzli 1983; Harbourne 1988). Hares therefore may have developed a mechanism or mechanisms whereby phenols and/or other secondary metabolites are neutralised. Another possible conclusion that could be drawn is that the levels found of the various secondary metabolites are not sufficient to act as deterrents, and this may well be the case. The toxicity of a chemical is always relative, depending on the dose taken in a given time period, the age and state of health of the animal, the mechanism of absorbtion and mode of excretion (Harbourne 1977). Bryant (1981) has shown that phenolics and terpenes act as effective deterents to Tassel eared Squirrels. Sinclair et al (1988) found that camphor in juvenile spruce extracts deterred feeding by snowshoe hares and Sinclair and Smith (1984) found that these hares consistently selected twigs low in resins or phenols. Tahvanainen et al (1985) found a negative correlation between phenolic glycoside concentration and food choice by mountain hares. Bryant (1979) in a review of previous results states that feeding is controlled by plant antiherbivore chemistry rather than plant proximal nutritional quality or fibre fraction. It would appear from this extensive and apparently conclusive information that secondary metabolites are often the determining factor in food selection by hares and other animals. However, all of these North American studies were conducted in areas where the hares were feeding almost exclusively on trees (especially willow, poplar and coniferous species) which could be expected to contain much higher amounts and much more virulent types of secondary compounds than any of the non-woody plants found in this study. It was noted during the study that there was no evidence of browsing on small shrub species such as *Hebe pimelioides* and data from the gut sample analysis also showed very low levels of consumption of these species. *H. pimelioides* and many of the other small shrub species are moderately aromatic and the occurrence of more potent secondary metabolites may be the reason for their avoidance.

The digestibility analyses gave comparative results for the different food items more in agreement with what was expected from the results of the diet study. The fact that *Hieracium* was the most digestible of the five food items was in agreement with the diet study results, but the magnitude of the difference was unexpected.

The ranking of the species (Table 4.9) was also in agreement with what was expected from the diet results, with the two relatively avoided food items (Rhacomitrium and Festuca) showing high fibre contents.

In this study neutral detergent fibre analysis results generally reflect the levels of consumption of the major food items. Bergeron and Jodoin (1987) found that meadow voles consumed greatest quantities of those plants with the lowest levels of fibre. However, Pehrson (1979), working with caged mountain hares, states that food selection appears to be influenced by factors other than digestibility and nutrient content, as does Bryant (1979). But choice of food items based on their digestibility would appear to be intuitively logical, because the nutritive value of a food is dependent on its chemical and structural composition, which together interact with the digestive and metabolic capacities of an animal (Robbins et al 1975). Therefore a food item that is high in digestibility could yeild a greater amount of energy to the animal than a similar calorific value food item of low digestibility. The results from this study indicate that this situation is occurring (Table 4.9). Belovsky (1986), in a paper summarising the data of 45 studies on 20 species of generalist herbivores, found that herbivores can be shown to choose their food based upon a minimum digestibility that determines energy value and a minimum item size or abundance that determines cropping rate (conflicting with the findings of Bryant (1979) and Pehrson (1979)). *H. pilosella* does not have the highest calorific value of the food plants investigated, but it is the most digestible and has a high availability. Therefore the calorific yield per gram from *Hieracium* would be much greater than the yield from any of the other four plants measured and the energy expended in gathering enough *Hieracium* to satisfy the animal would be minimal. The other four plant types (grasses, *Festuca*, *Poa* and *Rhacomitrium*) had much the same calorific and digestibility value as each other and, as would be expected, they are consumed in much the same quantities, except *Rhacomitrium* which is avoided. This is supported by comparing the monthly diet of hares and the calorific value of the food plants (Figs 4.1 & 4.13). During May the calorific value of *Hieracium* decreased and there was a concurrent increase in consumption of *Hieracium* at this time. It can be expected that hares, like most animals, require a variation in diet to satisfy all their nutritional requirements. Therefore hares may consume other plants besides the major plant or plants in their habitat. The NDF analysis gave results that most closely reflected those of the gut sample analysis and it appears that the digestibility or NDF content of the most readily available food plants is having an effect on their choice by hares.

The case of *Rhacomitrium* is somewhat perplexing as the results of the digestibility and calorimetry analyses indicate no reasons for its avoidance, while the secondary metabolite analyses results showed it to have the lowest content of phenols and tannins. Horne (1978) found that moss was eaten in increasing quantities with increasing altitude, perhaps indicating avoidance until other more preferred species become scarce. Switching to Rhacomitrium as a last resort can be supported by the results from this study also, due to the low consumption during spring, summer and autumn when other plants are relatively more abundant, and the increase in consumption during winter when other plants are relatively more scarce. This is consistent with the hypothesis that diets should expand when food is scarce and contract when food is abundant (MacArthur and Pianka 1966). The chemical composition of Rhacomitrium may have some effect on its avoidance by hares. However, Horne (1978) found no basis for selection or avoidance of any of the species tested due to chemical composition. Water content of Rhacomitrium may also have an effect on its choice as a food item because during winter when it is consumed in the greatest amounts, it also appears to have the highest water content (pers obs.).

In summary, it would appear that hares in this region rely heavily on H. pilosella for the major portion of their diet. The tussocks and grasses make up the majority of the remaining food and R. lanuginosum is avoided. The species eaten in the greatest amounts are those that are most available in the habitat ie. they are the dominant plants in the vegetation association. Secondary metabolites do not appear to be affecting the choice of any of the four most commonly eaten items, although they may be causing the avoidance of very seldom eaten plants such as the low, ground hugging, more aromatic shrubs. Calorific values do not seem to be affecting food choice either. However, digestibility is apparently influencing the choice of food by the hares in this area, particularly as regards Hieracium.

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APPENDIX 1

FAA - Killing and preserving fluid.

Ethyl alcohol	95%	50ml
Glacial acetic acid		5ml
Formaldehyde	37-40%	10ml
Water		35ml

Thin leaves are killed and hardened in 12 hours, thick leaves and stems need at least 24 hours. Sections don't need to be washed after FAA treatment.

APPENDIX 2.

NEUTRAL DETERGENT FIBRE REAGENT (10 litres)

190g Sodium EDTA
270g Ammonium pentaborate
300g Sodium lauryl sulphate

Dissolve the chemicals in distilled water using a magnetic stirrer (some heat may be required). Make up to 10 litres and store in plastic container with spigot.